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A THEORY OF *T-S* CURVES AS A METHOD FOR STUDYING THE MIXING OF WATER MASSES IN THE SEA[1]

By

W. B. STOCKMAN

Laboratory of Oceanology, Academy of Science, U. S. S. R.

A sea or an ocean, according to Defant (1929), is composed of water masses which are more or less homogeneous volumes of water characterized by definite relationships of physico-chemical properties such as temperature and salinity. No less interesting than the important problem of the origin of different water masses is the study of their transformation by the processes of mixing. The so-called method of *T-S* diagrams of Helland-Hansen (1918) have proved to be very useful in this respect. According to this method, temperature (ϑ) and salinity (s) of sea water are expressed as rectangular coordinates in relation to two parameters: depth (z) and time (t). Thus, $s = f(\vartheta, z, t)$. The lines, which on the *T-S* diagram correspond to a constant value of the parameter t, will be referred to as *T-S* curves.

Although the method of *T-S* diagrams is widely used in oceanographic practice, there is as yet no satisfactory theoretical treatment of the subject. In this study an attempt is made to set up the foundations of an analytical theory of *T-S* curves which gives a deeper insight into the essentials of this interesting method. A series of theorems is established which forms the basis of a distinctive "geometry of *T-S* curves" and which can be applied practically. A study is made of the well known method of Jacobsen (1927) for determining the coefficient of convectivity by means of *T-S* curves, and it is shown that

[1] Proofs not seen by author.

there is an error of principle in its geometrical part. The error can be avoided, however, by a deduction (from the basic formula of Jacobsen) which is developed and which is based on demonstrated geometrical properties of *T-S* curves. Finally, a new and simple geometrical method is developed for determining the coefficient of convectivity by means of *T-S* curves.

I. GEOMETRICAL PROPERTIES OF *T-S* CURVES IN THE MIXING OF THREE WATER MASSES

Let us consider the vertical mixing of three water masses in which the intermediate one is limited, and let us locate the plane $z = 0$ in the center of this intermediate water mass, whose boundaries are determined by values $z = \pm h$. The other two water masses are unlimited, extending from $z = h$ to $z = \infty$ and from $z = -h$ to $z = -\infty$. Since we consider here only processes of vertical heat conductivity and diffusion, which tend to equalize the temperature and salinity of water masses, we shall describe these processes by differential equations of the Fourier's type,

$$(1) \qquad \frac{\partial \vartheta}{\partial t} = K\frac{\partial^2 \vartheta}{\partial z^2}; \frac{\partial s}{\partial t} = K\frac{\partial^2 s}{\partial z^2},$$

assuming that the coefficient of turbulent mixing K in the region of all three water masses remains constant and is similar for the exchange of both salt and thermal properties.

Let us also assume at the initial moment that the temperature and salinity of the water masses are equal to

$$(2) \qquad \begin{aligned} &1) \text{ for } \infty > z > h && \vartheta = \Theta_1,\ s = S_1, \\ &2) \text{ for } h > z > -h && \vartheta = \Theta_2,\ s = S_2, \\ &3) \text{ for } -h > z > -\infty && \vartheta = \Theta_3,\ s = S_3. \end{aligned}$$

Evidently the initial condition is represented on the *T-S* diagram by three points with coordinates Θ_1, S_1; Θ_2, S_2; and Θ_3, S_3, forming a "triangle of mixing." This conception is fundamental for the whole subsequent theory of *T-S* curves.

Apart from the initial conditions (2), the solution of equations (1) must be subordinated to conditions of continuity of heat and salt exchange at the interfaces of the water masses, *i. e.*,

$$(3) \qquad \left(K\frac{\partial \vartheta}{\partial z}\right)^{\mathrm{I}}_{z=h} = \left(K\frac{\partial \vartheta}{\partial z}\right)^{\mathrm{II}}_{z=h}; \quad \left(K\frac{\partial \vartheta}{\partial z}\right)^{\mathrm{II}}_{z=-h} = \left(K\frac{\partial \vartheta}{\partial z}\right)^{\mathrm{III}}_{z=-h}$$

$$\vartheta^{\mathrm{I}}{}_{z=h} = \vartheta^{\mathrm{II}}{}_{z=h}; \quad \vartheta^{\mathrm{III}}{}_{z=-h} = \vartheta^{\mathrm{II}}{}_{z=-h},$$

and similarly for salinity. In the case of temperature the solutions of equations (1) will be:

for the region $\infty > z > h$ (water mass I)

$$(4)\quad \vartheta = \tfrac{1}{2}\left[\Theta_1+\Theta_3+(\Theta_1-\Theta_2)\Phi\left(\frac{z-h}{2\sqrt{Kt}}\right)+(\Theta_2-\Theta_3)\Phi\left(\frac{z+h}{2\sqrt{Kt}}\right)\right],$$

for the region $h > z > -h$ (water mass II)

$$(4')\quad \vartheta = \tfrac{1}{2}\left[\Theta_1+\Theta_3-(\Theta_1-\Theta_2)\Phi\left(-\frac{z-h}{2\sqrt{Kt}}\right)+(\Theta_2-\Theta_3)\Phi\left(\frac{z+h}{2\sqrt{Kt}}\right)\right],$$

for the region $-h > z > -\infty$ (water mass III)

$$(4'')\quad \vartheta = \tfrac{1}{2}\left[\Theta_1+\Theta_3-(\Theta_1-\Theta_2)\Phi\left(-\frac{z-h}{2\sqrt{Kt}}\right)-(\Theta_2-\Theta_3)\Phi\left(-\frac{z+h}{2\sqrt{Kt}}\right)\right].$$

In these formulas (4), $\Phi(\ )$ stands for Gauss' integral of errors (function of probabilities)

$$\Phi(x) = \frac{2}{\pi}\int_0^x e^{-\eta^2}d\eta .$$

The formulas for salinity are analogous (4). An analysis of the formulas of this type (4) will make it possible to establish a series of important deductions referring to the geometrical properties of *T-S* curves.

First of all it should be noted that $\Phi(\infty) = 1$. Therefore at $t = 0$ the temperature and salinity at the limits of the intermediate water mass II are equal respectively to half the sums of the temperatures and of the salinities adjoining the given limit:

$$(5)\quad \vartheta_{z=h} = \frac{\Theta_1+\Theta_2}{2}\ ;\ s_{z=h} = \frac{S_1+S_2}{2}$$

$$\vartheta_{z=-h} = \frac{\Theta_2+\Theta_3}{2}\ ;\ s_{z=-h} = \frac{S_2+S_3}{2}.$$

The latter values evidently correspond to the initial values of temperature and salinity established at the interface between two limited or unlimited water masses. However, as seen from formulas (4), with an increase of time (t) the intermediate layer degenerates, and temperatures and salinities of the three water masses tend to reach new stationary values,

$$\text{limit}\ (\vartheta)_{t\to\infty} = \frac{\Theta_1+\Theta_3}{2}\ ;\ \text{limit}\ (s)_{t\to\infty} = \frac{S_1+S_3}{2},$$

corresponding to the final stage of mixing.

Let us now follow the transformation in the system $s = f(\vartheta)$ of the "nucleus" of the intermediate water mass II, defining this term as the central region corresponding to a value of parameter $z = 0$. On the basis of the second formula (4), assuming $z = 0$, we obtain the following expression for the temperature of the "nucleus,"

$$\vartheta = \frac{\Theta_1 + \Theta_3}{2} + \Phi\left(\frac{h}{2\sqrt{Kt}}\right)\left(\Theta_2 - \frac{\Theta_3 + \Theta_1}{2}\right), \tag{6}$$

and we obtain an analogous formula for salinity:

$$s = \frac{S_1 + S_3}{2} + \Phi\left(\frac{h}{2\sqrt{Kt}}\right)\left(S_2 - \frac{S_3 + S_1}{2}\right). \tag{7}$$

Excluding the function $\Phi(\ )$ from (6) and (7), we obtain an equation that characterizes the transformation of the "nucleus" of water mass II in the system $s = f(\vartheta)$,

$$s - \frac{S_1 + S_3}{2} = \frac{S_2 - \dfrac{S_1 + S_3}{2}}{\Theta_2 - \dfrac{\Theta_1 + \Theta_3}{2}}\left(\vartheta - \frac{\Theta_1 + \Theta_3}{2}\right). \tag{8}$$

This formula (8) is nothing more than an equation for a straight line passing through two points: point II (Fig. 1) with coordinates Θ_2, S_2 and point P with coordinates $\dfrac{\Theta_1 + \Theta_3}{2}, \dfrac{S_1 + S_3}{2}$. In Fig. 1 the scheme of transformation of the water masses is indicated by arrows. The straight line II P, which is "the principal median" of the triangle of mixing I II III, divides its plane into a positive and a negative region. The results obtained are summarized by the following theorem:

1. *The geometrical position of points with a value of parameter* $z = 0$, *characterizing the transformation of the "nucleus" of the intermediate water mass with the course of time, represents the principal median of the triangle of mixing drawn from that apex of the triangle which corresponds to the intermediate water mass.*

Now let us determine the slope of the tangent to the *T-S* curve. Since the temperature is a function of two variables, s and z, at every point of the *T-S* curve, the slope of the tangent at any point of the *T-S* curve may be computed according to formula

$$\frac{d\vartheta}{ds} = \frac{\partial\vartheta}{\partial z} \Big/ \frac{\partial s}{\partial z}. \tag{9}$$

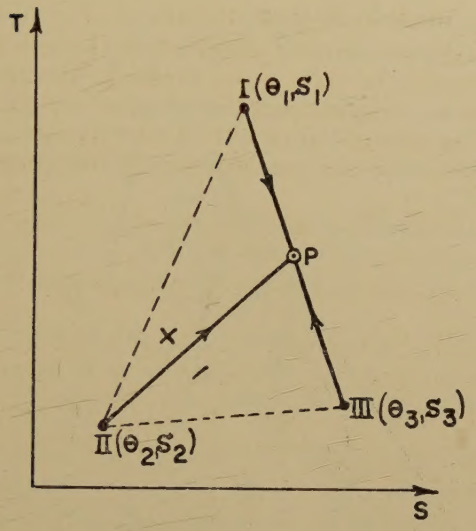


Figure 1.

Constructing $\frac{\partial \vartheta}{\partial z}$ and $\frac{\partial s}{\partial z}$ comparably to expressions of type (4), after some simple transformations we obtain, according to (9),

$$\frac{d\vartheta}{ds} = \frac{\Theta_1 - \Theta_2 + (\Theta_2 - \Theta_3)\, e^{-\frac{hz}{Kt}}}{S_1 - S_2 + (S_2 - S_3)\, e^{-\frac{hz}{Kt}}}, \tag{10}$$

from which it follows that, at the initial moment of mixing, when t is very small and $\frac{hz}{Kt}$ very high, the slope of the T-S curve for the region $z > 0$ is determined by expression

$$\frac{d\vartheta}{ds} = \frac{\Theta_1 - \Theta_2}{S_1 - S_2} = \text{Constant} \tag{11}$$

and for the region $z < 0$ by expression

$$\frac{d\vartheta}{ds} = \frac{\Theta_2 - \Theta_3}{S_2 - S_3} = \text{Constant.} \tag{12}$$

Thus, at the initial moment of mixing the T-S curve is characterized by straight lines, which on the T-S diagram consecutively connect the water masses I–II, II–III, as shown by the broken line in Fig. 2.

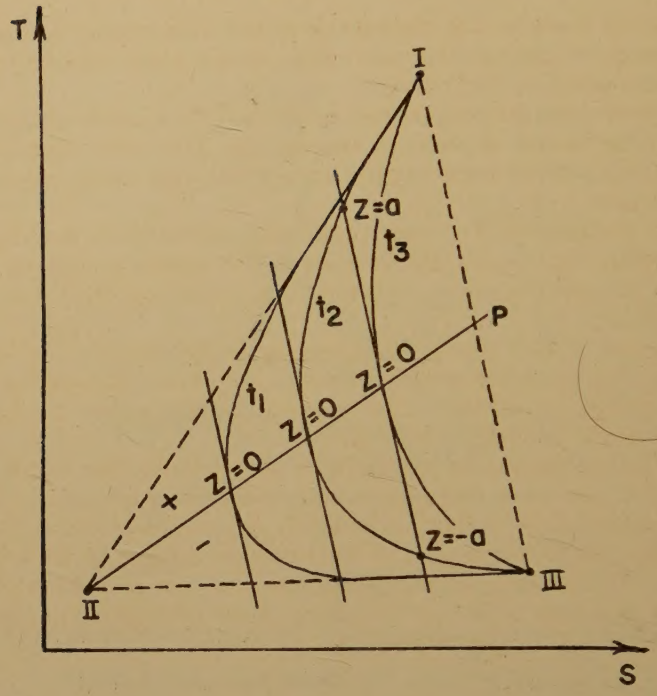


Figure 2.

It is also obvious from formulas (4) and (10) that, at t = Constant, the branches of the T-S curve asymptotically approach these same straight lines I–II, II–III as z increases, *i. e.*, with increasing distance from the central region of the intermediate water mass. This approach is the more rapid the greater the width ($2h$) of the intermediate water mass, or the lower the value of t (for given values of h and z).

And finally, it follows from formula (10) that the slope of the tangent at points of the T-S curve corresponding to the "nucleus" of the intermediate water mass (*i. e.*, at points with a value of parameter $z = 0$) is determined by the expression

$$\left(\frac{d\vartheta}{ds}\right)_0 = \frac{\Theta_1 - \Theta_3}{S_1 - S_3} = \text{Constant.} \tag{13}$$

This signifies that tangents drawn through the points mentioned are parallel to the side of the triangle of mixing which is opposite to the intermediate water mass (Fig. 2). This side will be named the *base of the triangle of mixing.* Since the slope of the T-S curve, when

crossing the point $z = 0$, changes direction with respect to the base of the triangle of mixing, this point in a certain sense may be called the maximum point of *T-S* curves.

Our deduction can be summed up in the following theorems:

2. *At the initial moment of mixing, the T-S curve consists of two straight lines which consecutively connect the given water masses on the T-S diagram.*

3. *At points of the T-S curves sufficiently distant from the limits of the intermediate water mass, the tangents to T-S curves practically coincide with the straight lines, which consecutively connect the three water masses considered.*

4. *Points of T-S curves corresponding to the "nucleus" of the intermediate water mass are extreme points of T-S curves in respect to the base of the triangle of mixing. The tangents at these points are parallel to the base of the triangle of mixing.*

Now let us determine the slope of the straight line which, on the *T-S* curve, connects two points with values of parameter z that are equal but opposite in sign. Evidently these points of the *T-S* curve are located on different sides of the principal median of the triangle of mixing. If the value of the parameter z at the points considered is equal, $z = a$ and $z = -a$, the slope of the straight line connecting these points will be determined by the formula

$$tg\alpha = \frac{\vartheta_a - \vartheta_{-a}}{S_a - S_{-a}}.$$

By substituting alternatively values $z = a$ and $z = -a$ in formulas (4) and by simple transformations we obtain

$$\vartheta_a - \vartheta_{-a} = \frac{\Theta_1 - \Theta_3}{2}\left[\Phi\left(\frac{a-h}{2\sqrt{Kt}}\right) + \Phi\left(\frac{a+h}{2\sqrt{Kt}}\right)\right]$$

$$s_a - s_{-a} = \frac{S_1 - S_3}{2}\left[\Phi\left(\frac{a-h}{2\sqrt{Kt}}\right) + \Phi\left(\frac{a+h}{2\sqrt{Kt}}\right)\right];$$

hence

$$tg\alpha = \frac{\Theta_1 - \Theta_3}{S_1 - S_3}.$$

Thus we may regard as demonstrated the theorem:

5. *Straight lines, which on a T-S curve connect two points having identical values of parameter z but with opposite signs, are parallel to the base of the triangle of mixing.*

Combining this theorem with theorem 4 we obtain a new deduction:

6. *A tangent, drawn at the point of intersection of the principal median of the triangle of mixing with the T-S curve, locates on the other T-S*

curve, prior in time, two points having equal values of the parameter z but with opposite signs.

From formula (4) issues another no less remarkable property possessed by points of a *T-S* curve with a parameter value of $z = \pm h$, i. e., points located on the boundaries of the intermediate water mass. To demonstrate this let us consider two points Q and D with an identical value of parameter $z = h$ but with different values of parameter $t = t'$ and $t = t''$ belonging to two successive *T-S* curves (Fig. 3).

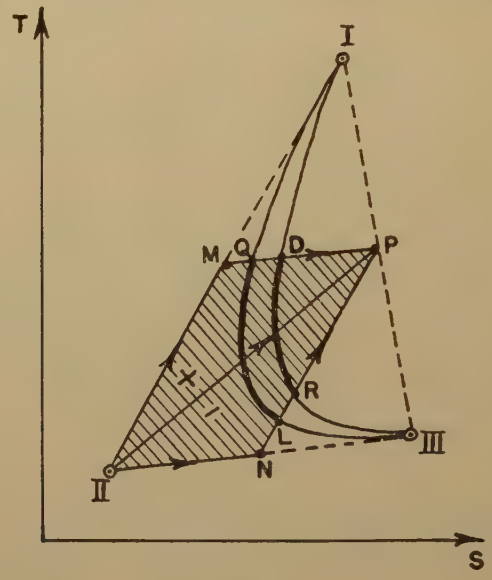


Figure 3.

The equation of a straight line passing through points Q (h, t') and D (h, t'') is written as follows:

$$\vartheta - \vartheta(h, t') = \frac{\vartheta(h, t') - \vartheta(h, t'')}{s(h, t') - s(h, t'')} [s - s(h, t')].$$

Substituting values for ϑ and s from formulas of type (4) we obtain:

$$(14) \quad \vartheta - \frac{\Theta_1 + \Theta_3}{2} - \frac{\Theta_2 - \Theta_3}{2} \Phi\left(\frac{h}{\sqrt{Kt'}}\right) = \frac{\Theta_2 - \Theta_3}{S_2 - S_3} \left[s - \frac{S_1 + S_3}{2} - \frac{S_2 - S_3}{2} \Phi\left(\frac{h}{\sqrt{Kt'}}\right) \right].$$

It follows from equation (14) that the straight line considered is parallel to side II–III of the triangle of mixing, since the slope m of this straight line is equal to:

$$m = \frac{\Theta_2 - \Theta_3}{S_2 - S_3}.$$

In an analogous way we discover that the straight line passing through points L $(-h, t')$ and R $(-h, t'')$ (Fig. 3) is parallel to side I–II of the triangle of mixing. On the basis of equation (14) it is easy to show that the straight line which passes through points Q and D passes also through point P located in the middle of the base of the triangle of mixing. But if so, the straight line considered also passes through point M lying in the middle of side I–II of the triangle of mixing.

In exactly the same way can we demonstrate that the straight line passing through points L and R also passes through points P and N (Fig. 3). But, as already established in formulas (5), points M $\left(\frac{\Theta_1 + \Theta_2}{2}, \frac{S_1 + S_2}{2}\right)$ and N $\left(\frac{\Theta_2 + \Theta_3}{2}, \frac{S_2 + S_3}{2}\right)$ characterize the properties of water on the boundaries of the intermediate layer at the initial moment of mixing, these properties varying continuously with time.

Now we come to the conclusion that this process is illustrated on the *T-S* curve by two straight lines MP and NP which are medians of the triangles IPII and IIPIII; to distinguish them from the principal median they will be referred to as "secondary" medians of the triangle of mixing.

It is obvious that any point within the parallelogram IINMP, shown by hatched lines in Fig. 3, will characterize the water of the intermediate layer.

Thus this parallelogram may be regarded as a distinctive geometrical interpretation of the transformation of the intermediate water layer, and it should be kept in mind that on the boundaries of this layer the passage from point II to points M and N occurs instantaneously, whereas further transformation along the secondary medians proceeds continuously with time t. The secondary medians of the triangle of mixing cut off arcs on the successive *T-S* curves; every point of these arcs corresponds to the water of the intermediate layer in the system $s = f(\vartheta)$. These results may be summed up in the form of the following theorem:

7. *All points in the system* $s = f(\vartheta)$ *corresponding to the water on the boundaries of the intermediate layer lie on the secondary medians of the triangle of mixing. The secondary medians cut off, on the T-S curves,*

arcs which correspond to the water of the intermediate layer in the system $s = f(\vartheta)$.

The theorems here demonstrated are of interest, not only in respect to an abstract "geometry of T-S curves," but because they are also of practical value. Thus, on the basis of theorem 3 we are often able to reconstruct initial thermohaline indices of the intermediate water mass. For this purpose, according to the above theo-

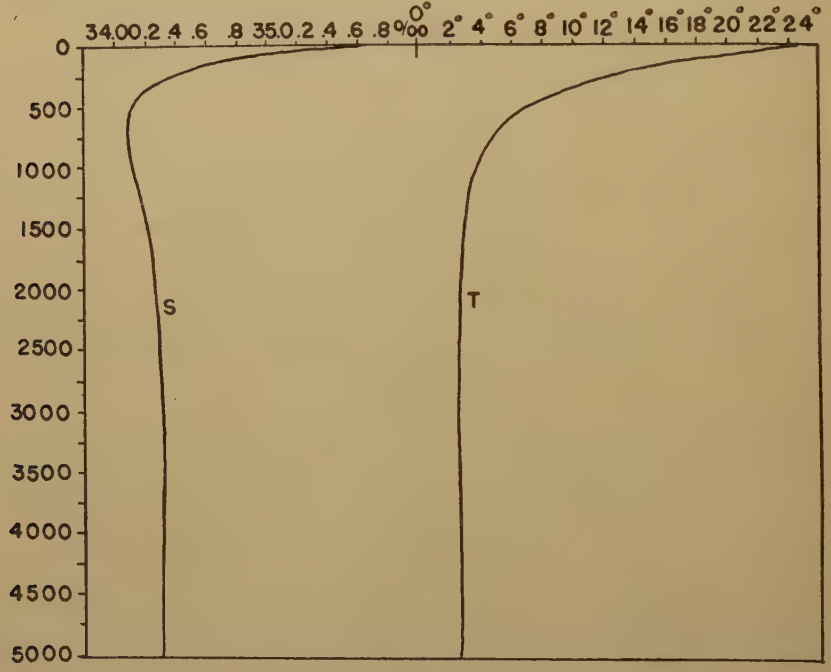
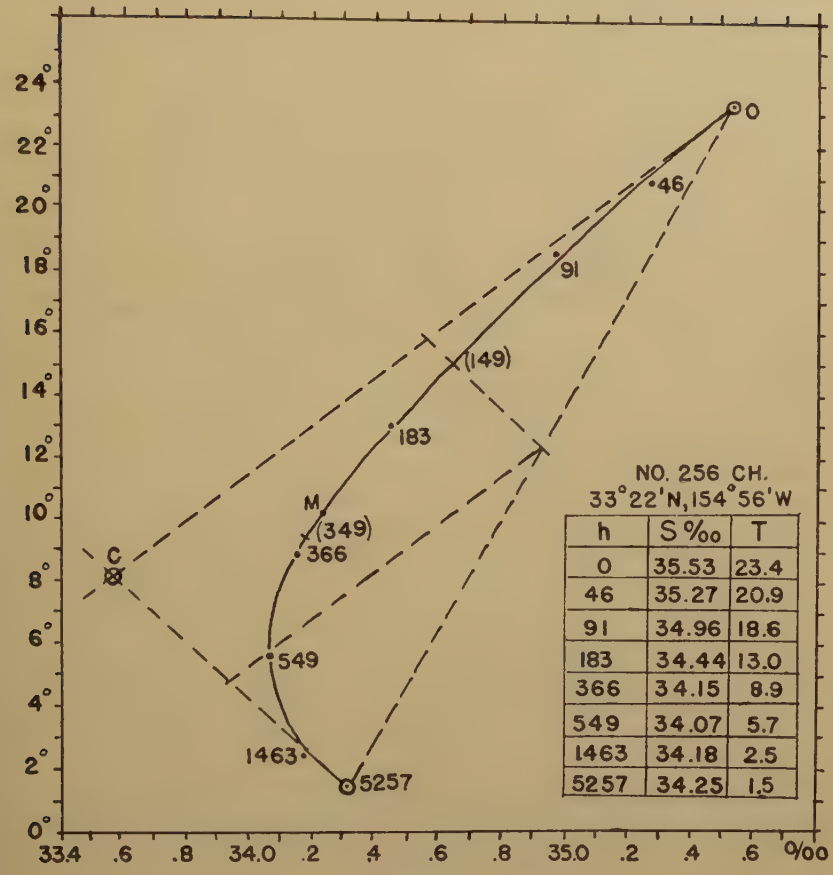


Figure 4.

rem, tangents must be drawn at points of the T-S curve of the type considered sufficiently distant from the region of its rounding, or, in other words, prolongations of the rectilinear branches of the curve. The intersection of such straight lines will determine the coordinates of the point corresponding to the temperature and salinity of the intermediate water mass.

Theorem 7 is of no less practical value. Up to now in oceanographic investigations the question has remained open as to the vertical dimensions of water masses which could be detected in the sea by the method of T-S curves. The conclusions of marine scientists regarding



h	S ‰	T
0	35.53	23.4
46	35.27	20.9
91	34.96	18.6
183	34.44	13.0
366	34.15	8.9
549	34.07	5.7
1463	34.18	2.5
5257	34.25	1.5

Figure 5.

the vertical limits of some layer or other were rather vague and conventional. This is accounted for by the continuous character of the vertical distribution of different properties of sea water, owing to a levelling effect exercised by processes of mixing.

For example, Fig. 4 shows the curves of vertical temperature and salinity distribution in the central Pacific Ocean, plotted by Wüst (1929) on the basis of data from the "Challenger" expedition, station ch. 256. We see immediately the difficulties that arise from the attempt to determine, by means of these data alone, the vertical limits of the layer of fresh subarctic water, whose presence is clearly shown by the peculiar curvature of the vertical salinity distribution

curve. These difficulties can be easily avoided with the help of theorem 7. For this purpose, it is necessary first of all to restore by the *T-S* curve the primary thermohaline indices of the water masses, or, in other words, to construct a triangle of mixing. Then we must determine the depth of the points of intersection of secondary medians of the triangle of mixing with the given *T-S* curve. These depths, according to theorem 7, correspond to the upper and lower limits of the intermediate layer of subarctic water.

Fig. 5 shows the *T-S* curve constructed by Wüst (1929); this corresponds to the vertical temperature and salinity distribution in Fig. 4. In Fig. 5 are also given all the necessary constructions.

We see that secondary medians intersect the *T-S* curve at points with depth values of 549 and 149 m. The latter was obtained by linear interpolation of depths along the *T-S* curve. The depths mentioned are the sought-for limits of the intermediate subarctic layer. Obviously, the result of the construction used will be exact as far as the propositions demonstrated above are correct under actual conditions in the sea. It must be remembered that, strictly speaking, the theorems mentioned are correct only in the absence of an upper (sea surface) and a lower (sea bottom) limit. Practically, this signifies that the width of the intermediate layer should be much less than the total depth of the sea, and the "nucleus" of the intermediate water layer about an equal distance between surface and bottom, where, for one reason or another, temperature and salinity distribution do not depend on time.

At any rate, an adequate criterion of the reliability of determinations of the thickness of the intermediate layer is furnished by the degree of accuracy with which the demonstrated theorems on the geometrical properties of *T-S* curves can be applied to practical circumstances. Thus, on the basis of these theorems, it should be expected that the point of intersection of the principal median with the empirical *T-S* curve shown on Fig. 5 will be situated at an equal distance (with respect to depth z) from the points of intersection of the secondary medians with the same *T-S* curve. The point of intersection of the principal median with the *T-S* curve on Fig. 5 (point M) corresponds to a depth of 307 m. The latter does not quite correspond to the center of the intermediate layer, whose depth is 349 m. and whose position (with respect to parameter z) is indicated in the figure by a straight line drawn across the curve. However, there is no great discrepancy between the depth of point M (307 m.) and the center of the intermediate layer (349 m.), the relative value of the error in this case not exceeding 12 per cent. Thus the demonstrated propositions used in the determination of the thickness of the inter-

mediate water mass in the Pacific are proved to give fairly accurate estimates.

However, it must be observed that the conception of water masses being discrete bodies of water, which, prior to mixing possess individual properties (a conception that is both fundamental to the whole theory of *T-S* curves and very useful in oceanography) is a rather conventional one. Indeed, we can obtain a precise reproduction of this conception by placing in a vessel several layers of a liquid, one above the other, and observing the gradual levelling of their properties, interpreting this process by means of *T-S* curves. Obviously a similar temperature and salinity distribution could be obtained in the case of a vessel primarily containing non-stratified water with identical properties at every point within the vessel.

This could be accomplished by changing the properties of the water by means of external influences, *i. e.*, subjecting the water on the surface to warming, cooling, or to a change in salinity brought about by rainfall or evaporation at the surface. As a result of the external influences mentioned, together with mixing processes, we might obtain in our vessel a vertical temperature and salinity distribution identical with that reached in the former case (intermixing of several layers, individual at the initial moment), although in the latter case such layers (water masses) at the initial moment were nonexistent.

Since in the author's opinion there are, strictly speaking, no water masses in nature, excepting perhaps the fresh water on land and salt water of the world oceans (merely two), it must be kept in mind that in dissecting oceanic water into different water masses we deal with layers which in reality are nonexistent in the sea. Nevertheless, this abstract conception of water masses, forming the basis of the theory of *T-S* curves, and analogous to the conception of aerial masses, plays a useful part like many other abstract conceptions of precise natural science.

II. DETERMINATION OF THE COEFFICIENT OF MIXING BY MEANS OF *T-S* CURVES (ON THE CORRECTNESS OF JACOBSEN'S METHOD)

T-S curves serve not only to determine the structure of water masses in the sea, but, as shown by Jacobsen (1927), they enable computation of the coefficient of turbulent mixing in the sea. The essentials of the method are as follows: one of two curves is selected; one (later in respect to time), with a tangent drawn at the point of its maximum curvature, locates on the other *T-S* curve (that prior in time) two points with known values of parameters [z' and z''] $z = z'$

and $z = z''$. Then, by computing the difference of parameters we can calculate the coefficient K according to Jacobsen by the formula

$$K = \frac{(z' - z'')^2}{8\Delta t} \tag{15}$$

where Δt is the lapse of time separating the first T-S curve from the second.

Owing to its extreme simplicity, the ingenious method of Jacobsen has been widely applied in oceanography; this, however, cannot prevent us from expressing some doubts as to its correctness which arise as the result of a closer scrutiny of its theoretical foundations.

Indeed, beside the difficulties occasionally experienced in practice in determining the point of maximum curvature of a T-S curve and drawing a tangent, it must be kept in mind that the *curvature of a T-S curve varies considerably in relation to the scale of temperature and salinity on the T-S diagram.*

Obviously *the position of the point of maximum curvature of a T-S curve on such a deformed diagram does not correspond to its position in natural* (not distorted) *coordinates.* Nevertheless, this important fact is completely overlooked both in the theory of the method itself and in its practical applications. Moreover, even a detailed study of the fundamentals of the theory of Jacobsen's method fails to answer the question of whether drawing a tangent just at the point of maximum curvature is essential to the method itself, or whether the tangent could be as well drawn at any other point of the T-S curve.

It must be noted that the method of Jacobsen is applicable to the usual type of T-S curves in the case of the mixing of three water masses. Moreover, as seen from the theory of the method as stated by Jacobsen, the water medium is assumed to be unlimited (in his computations z is integrated within the limits $z = -\infty$ to $z = \infty$).

Thus the initial statements of Jacobsen's theory of procedure fully comply with the conditions of the problem considered in the foregoing chapter. Hence, we are able to use fully the demonstrated theorems on the geometrical properties of T-S curves for a more exact and very simple basis for a theory of Jacobsen's method.

For this purpose let us consider the two T-S curves illustrated in Fig. 6. The first is assumed to correspond to the moment of time t_0 and the second to $t_0 + \Delta t$. Let us then draw a tangent at point A having parameters $z = 0$, $t_0 + \Delta t$ and which consequently belongs to the second T-S curve; this tangent intersects the branches of the first curve at points B and C. According to theorem I of the first chapter, point A lies on the principal median IIE of the triangle of mixing and

forms at the same time the maximum point of the second *T-S* curve in relation to the base of the triangle of mixing.

On the other hand, according to theorems 5 and 6 of the same chapter, the tangent mentioned above must be parallel to the base of the triangle of mixing and points B and C must have equal values, but opposite in signs, of parameter z in relation to point D ($z = 0, t_\circ$). We emphasize that the last circumstance is essential to the following computations which finally lead to the formula of Jacobsen. According to the above let the parameters of points B and C, which belong to the first *T-S* curve, be characterized by values B $\left(-\frac{\Delta z}{2}, t_\circ\right)$, C $\left(\frac{\Delta z}{2}, t_\circ\right)$, where Δz is the difference of parameters z between the points B and C.

Let us assume, together with Jacobsen (1927) and Okada (1938), that temperature and salinity at points A, B, C can be presented precisely enough for practical purposes in the form of the sum of the first terms of Taylor's series,

$$(16)\qquad \begin{cases} \vartheta_C = \vartheta_\circ + \frac{\Delta z}{2}\left(\frac{\partial \vartheta}{\partial z}\right)_\circ + \frac{(\Delta z)^2}{8}\left(\frac{\partial^2 \vartheta}{\partial z^2}\right)_\circ \\ s_C = s_\circ + \frac{\Delta z}{2}\left(\frac{\partial s}{\partial z}\right)_\circ + \frac{(\Delta z)^2}{8}\left(\frac{\partial^2 s}{\partial z^2}\right)_\circ \\ \vartheta_B = \vartheta_\circ - \frac{\Delta z}{2}\left(\frac{\partial \vartheta}{\partial z}\right)_\circ + \frac{(\Delta z)^2}{8}\left(\frac{\partial^2 \vartheta}{\partial z^2}\right)_\circ \\ s_B = s_\circ - \frac{\Delta z}{2}\left(\frac{\partial s}{\partial z}\right)_\circ + \frac{(\Delta z)^2}{8}\left(\frac{\partial^2 s}{\partial z^2}\right)_\circ \\ \vartheta_A = \vartheta_\circ + \frac{\partial \vartheta}{\partial t}\Delta t;\ s_A = s_\circ + \frac{\partial s}{\partial t}\Delta t, \end{cases}$$

while the equation of tangent BC may be inscribed in the form of

$$(17)\qquad \vartheta_A - \vartheta_B = \left(\frac{d\vartheta}{ds}\right)_\circ (s_A - s_B)$$

where $\left(\frac{d\vartheta}{ds}\right)_\circ$ is the slope of the tangent to the *T-S* curve at point $z = 0$.

By substituting in formula (17) corresponding values from formula (16) and rearranging the terms we obtain

$$(18)\quad \left[\frac{\partial\vartheta}{\partial t}-\left(\frac{d\vartheta}{ds}\right)_0\left(\frac{\partial s}{\partial t}\right)\right]\Delta t=-\frac{\Delta z}{2}\left[\left(\frac{\partial\vartheta}{\partial z}\right)_0-\left(\frac{d\vartheta}{ds}\right)_0\left(\frac{\partial s}{\partial z}\right)_0\right]+\frac{(\Delta z)^2}{8}\left[\left(\frac{\partial^2\vartheta}{\partial z^2}\right)_0-\left(\frac{d\vartheta}{ds}\right)_0\left(\frac{\partial^2 s}{\partial z^2}\right)_0\right].$$

Let us now decipher the expressions in brackets [ ] from formula (18). On the basis of formula (9), the first bracket to the right of (18) is reduced to 0. Differentiating (9) by z as a complex function, we obtain

$$(19)\quad \frac{\partial^2\vartheta}{\partial z^2}=\frac{d^2\vartheta}{ds^2}\left(\frac{\partial s}{\partial z}\right)^2+\frac{d\vartheta}{ds}\left(\frac{\partial^2 s}{\partial z^2}\right).$$

Consequently the remaining item on the right of (18) can be inscribed as:

$$(20)\quad \frac{(\Delta z)^2}{8}\left[\left(\frac{\partial^2\vartheta}{\partial z^2}\right)_0-\left(\frac{d\vartheta}{ds}\right)_0\left(\frac{\partial^2 s}{\partial z^2}\right)_0\right]=\frac{(\Delta z)^2}{8}\left(\frac{d^2\vartheta}{ds^2}\right)_0\left(\frac{\partial s}{\partial z}\right)^2.$$

Combining equation (1) with formulas (9) and (19), it is easy to demonstrate that

$$\frac{\partial\vartheta}{\partial t}-\frac{d\vartheta}{ds}\frac{\partial s}{\partial t}=K\frac{d^2\vartheta}{ds^2}\left(\frac{\partial s}{\partial z}\right)^2.$$

Substituting the right hand side of this last equation for the brackets on the left of formula (18) and omitting index 0, we obtain

$$K\frac{d^2\vartheta}{ds^2}\left(\frac{\partial s}{\partial z}\right)^2\Delta t=\frac{(\Delta z)^2}{8}\left(\frac{d^2\vartheta}{ds^2}\right)\left(\frac{\partial s}{\partial z}\right)^2$$

or, finally

$$(21)\quad K=\frac{(\Delta z)^2}{8\Delta t}.$$

As we see, the last formula is identical with Jacobsen's.

An essential feature of our reasoning in deducing Jacobsen's formula is that we draw the tangent BC (Fig. 6), not at the point of maximum curvature, but *at the point of intersection of the principal median of the triangle of mixing with the second T-S curve.* Generally speaking, this point does not coincide with the point of maximum curvature as illustrated by Fig. 7, which shows two T-S curves constructed according to formula (4) on the proposition that: $\Theta_1 = 2°$, $S_1 = 34.00°/_{oo}$; $\Theta_2 = 1°$, $S_2 = 33.10°/_{oo}$; $\Theta_3 = 5°$, $S_3 = 33.20°/_{oo}$; $K = 10\ \frac{cm^2}{cl\ K}$; $2h = 120$ m. for two values of $t = 30$ days and $t = 50$ days. As seen

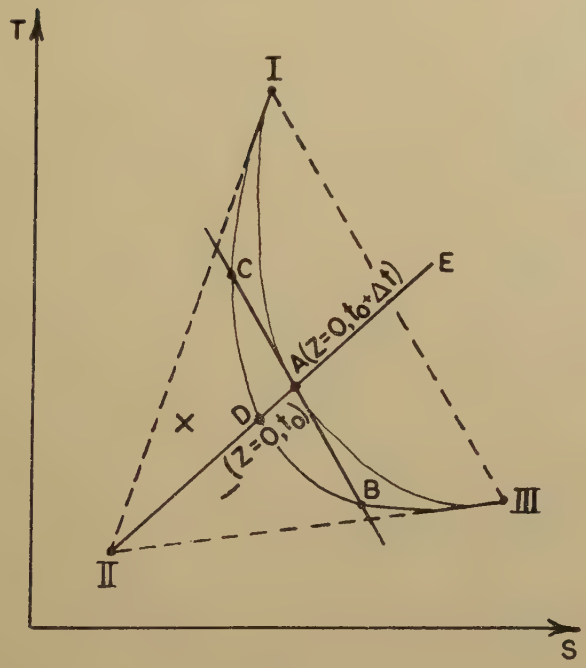


Figure 6.

from Fig. 7, the maximum curvature of the curve for $t = 50$ days lies in the vicinity of the point with parameter $z = 40$ m.

It is easily seen that Jacobsen's construction could be identical with ours only in one particular case; *i. e.*, when the triangle of mixing would be isosceles in relation to sides I–II and II–III (Fig. 6) and when, consequently, its principal median coincides with the axis of symmetry of the *T-S* curve (bisects the angle I, II, III). Since in this case the point of maximum curvature is actually located on the principal median (bisector) of the triangle of mixing, both constructions will have a completely identical significance. Jacobsen considered just this particular case, though he expected to obtain a method of determining the coefficient of mixing applicable to any case. Thus it is no wonder that the calculations of Jacobsen gave a result homotypical with formula (21). There is also no difficulty in discovering the cause of the error made by Jacobsen. The explanation is that the theory of Jacobsen completely ignores the important element of the triangle of mixing.

Contrary to our principle, Jacobsen sets no limits to the branches of

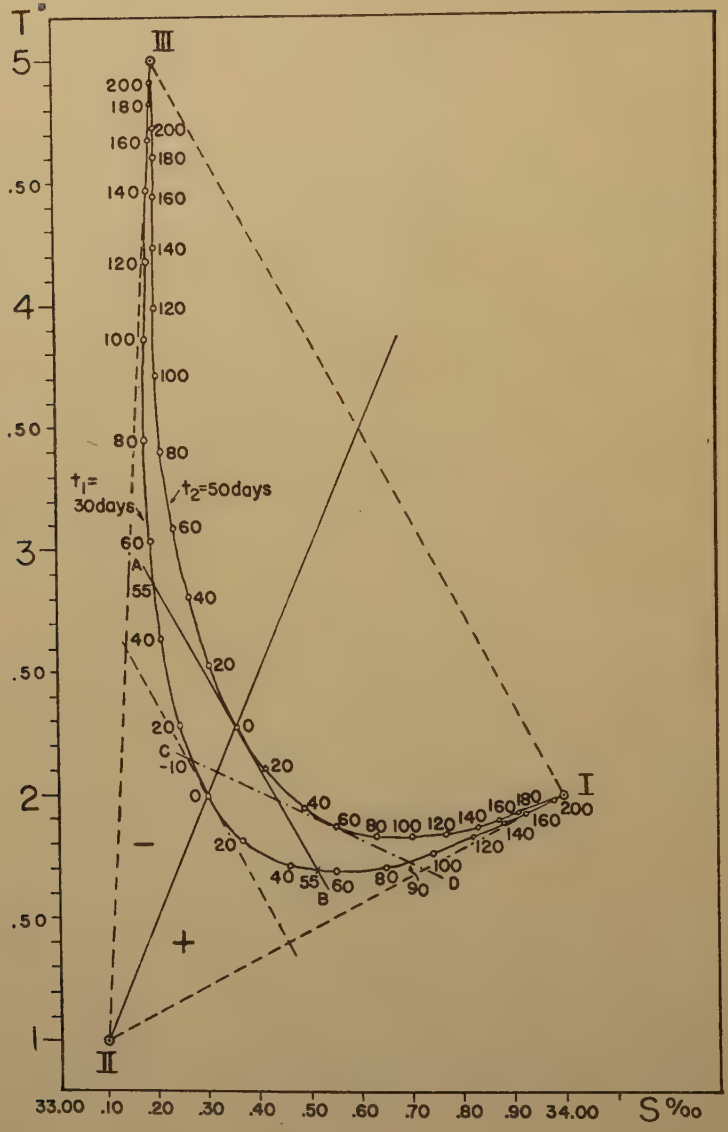

T°
5
.50
4
.50
3
.50
2
.50
1
III
II
I
200
180
160
140
120
100
80
60
40
20
0
-10
A
B
C
D
55
90
t_1= 30days
t_2=50days
+
−
33.00
.10
.20
.30
.40
.50
.60
.70
.80
.90
34.00
S‰

Figure 7.

the *T-S* curve, which have to break up at points corresponding to the extreme water masses. Evidently this important fact essentially affects the disposition of intermediate points on the *T-S* curve, which correspond to one or another value of parameter z. In excluding from the field of vision the totality of the water masses, Jacobsen naturally had at his disposition only that means of orientation which can be furnished by the axis of symmetry of a *T-S* curve with unlimited branches.

In order to elucidate fully the question of the validity of Jacobsen's method, let us consider whether it is possible to transform any triangle of mixing into an isosceles triangle. If such a transformation is possible by changing the scales along the rectangular axes *T-S*, then evidently the construction of Jacobsen can always be adjusted to the method indicated, so that both methods will give equally correct results independently of the scales selected.

Let us designate the coordinates of apices I, II, III of a given mixing triangle by $x_1, y_1; x_2, y_2; x_3, y_3$, respectively. Then, to obtain an answer to the above question we have to investigate the following indeterminate equation, whose both parts represent the lengths of sides I–II and II–III of the triangle of mixing:

$$(22) \quad \alpha^2 (x_1 - x_2)^2 + \beta^2 (y_1 - y_2)^2 = \alpha^2 (x_3 - x_2)^2 + \beta^2 (y_3 - y_2)^2 ,$$

where α and β are coefficients of proportionality of scales on the axes x and y (s and ϑ) respectively.

The last equation may easily be reduced to

$$\alpha^2 A + \beta^2 B = 0$$

where

$$A = (x_1 - x_2)^2 - (x_3 - x_2)^2; \quad B = (y_1 - y_2)^2 - (y_3 - y_2)^2 .$$

Consequently α is related to β by

$$(23) \qquad \alpha = \beta \sqrt{-\frac{B}{A}} .$$

Formula (23) indicates that transformation into an isosceles triangle is possible only in the case where the values A and B have *opposite* signs. On the contrary, in the case of similar signs such a transformation cannot be accomplished. That is why, generally speaking, the construction of Jacobsen is erroneous in its principle, whereas our mode of constructing a tangent, owing to the invariability of our constructions in relation to the scales of the *T-S* curve, is the only method valid in all cases of transformable and nontransformable (nonisosceles) triangles of mixing.

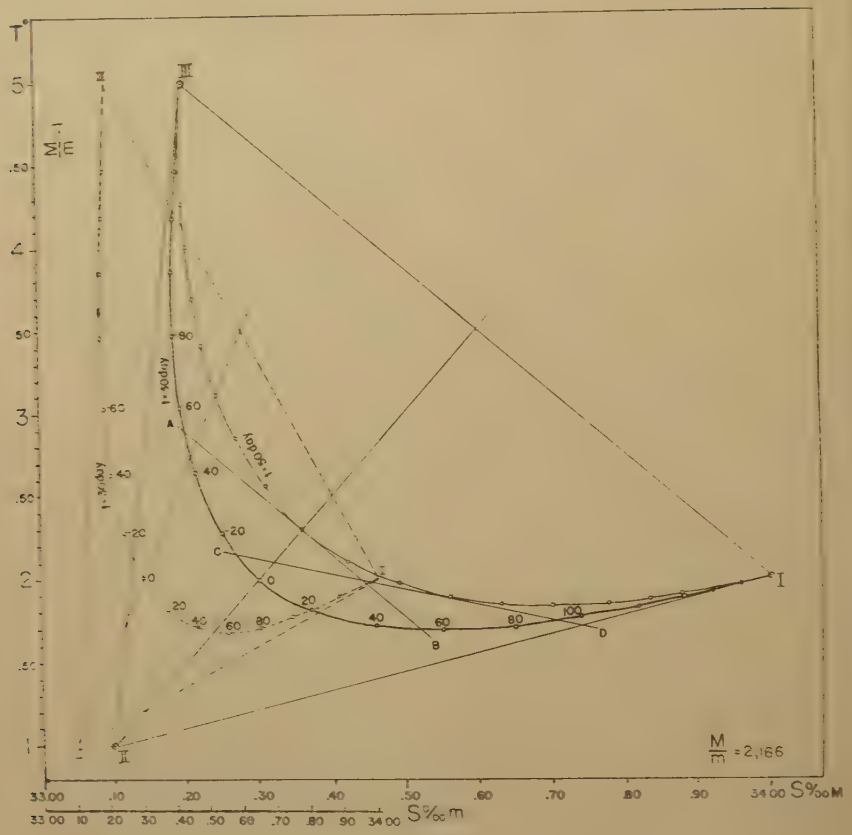


Figure 8.

Fig. 8 gives an example of the transformation of the triangle of mixing (illustrated in Fig. 7) into an isosceles triangle. It may easily be seen from formula (23) that in this case such a transformation is possible and can be accomplished by changing only one scale on the x axis (i. e., s) ($\beta = 1$), increasing the scale of salinity 2,166 times, as compared with the previous one ($\alpha = 2{,}166$).

Fig. 8 shows also what essential changes are brought about in the curvature of a T-S curve by changes of scales; thus, the point of maximum curvature ($z = 40$) of the dotted T-S curve, corresponding to the "original," with the change of scale is converted almost into the point of minimum curvature (with the same parameter $z = 40$ on the transformed curve). As is to be expected, the T-S curve changed by

the transformation of this triangle into an isosceles one becomes a symmetrical curve in relation to the principal median (bisector) of the triangle of mixing. Naturally, a tangent drawn at the point of maximum curvature of such a symmetrical *T-S* curve will be parallel to the base of the triangle of mixing, so that in this case the construction of Jacobsen will fully coincide with the construction required by the deduction of formula (21) and the theorems of Chapter I.

In contrast to this example, in Fig. 9 is shown a triangle of mixing with *T-S* curves constructed for $t = 30$ days and $t = 50$ days, which cannot be transformed into an isosceles triangle, as is easily proved by formula (22).

Finally, we suggest a new and simple graphical method for determining the coefficient of mixing with the help of *T-S* curves.

Indeed, as follows from formula (10), the slope of the tangent at the point corresponding to the limit of the intermediate layer (assuming $z = -h$) is determined for the period of time t_1 by the expression

$$tg\alpha_1 = \frac{\Theta_1 - \Theta_2 + (\Theta_2 - \Theta_3)\, e^{\frac{h^2}{Kt_1}}}{S_1 - S_2 + (S_2 - S_3)\, e^{\frac{h^2}{Kt_1}}}$$

and for the period of time t_2 by the expression,

$$tg\alpha_2 = \frac{\Theta_1 - \Theta_2 + (\Theta_2 - \Theta_3)\, e^{\frac{h^2}{Kt_2}}}{S_1 - S_2 + (S_2 - S_3)\, e^{\frac{h^2}{Kt_2}}}.$$

It follows from these formulas that

$$e^{\frac{h^2}{Kt_1}} = A\ ;\quad e^{\frac{h^2}{Kt_2}} = B\,, \tag{24}$$

where A and B are

$$\begin{cases} A = \dfrac{\Theta_1 - \Theta_2 - (S_1 - S_2)\, tg\alpha_1}{(S_2 - S_3)\, tg\alpha_1 - \Theta_2 + \Theta_3}\,; \\ B = \dfrac{\Theta_1 - \Theta_2 - (S_1 - S_2)\, tg\alpha_2}{(S_2 - S_3)\, tg\alpha_2 - \Theta_2 + \Theta_3}\,. \end{cases} \tag{25}$$

Taking the logarithm of (24) we obtain

$$t_1 = \frac{h^2}{KlnA}\ ;\quad t_2 = \frac{h_2}{KlnB}\,.$$

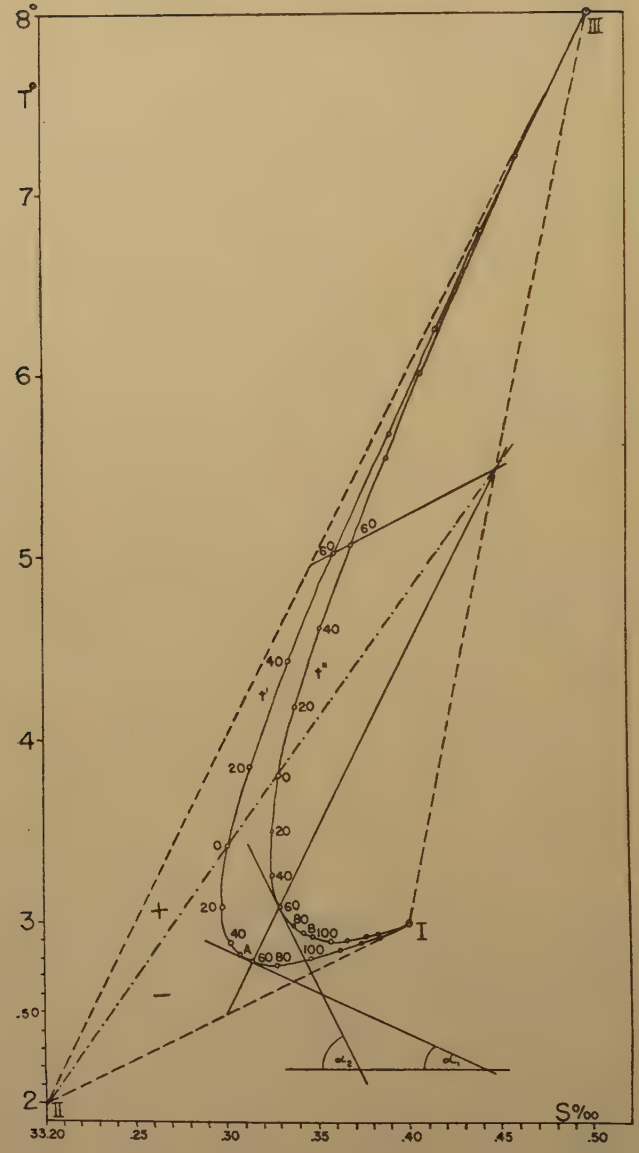


Figure 9.

Forming the difference $t_2 - t_1 = \Delta t$, we obtain

$$\Delta t = \frac{h^2}{K}\left(\frac{lnB - lnA}{lnB \cdot lnA}\right)$$

hence

$$K = \frac{h^2}{\Delta t}\left(\frac{lnB - lnA}{lnB \cdot lnA}\right). \tag{26}$$

This is the precise formula for computing the coefficient of mixing, instead of the approximate formula (21). The determination of parameter h on the basis of theorem 7 is quite simple. It must be kept in mind that h equals only one-half the thickness of the intermediate layer:

$$h = \frac{z'' - z'}{2}$$

where $z'' - z'$ is the difference of depths located on the T-S curve by the secondary medians of the triangle of mixing. Consequently, formula (26) can be inscribed more conveniently in the following form:

$$K = \frac{(z'' - z')^2 M}{4\Delta t}. \tag{26'}$$

It is interesting that formula (26′) somewhat resembles the approximate formula (21), though the significance of values $z'' - z'$ in both formulas is quite different. To calculate the multiplier M, we must draw tangents at the points of intersection of one of the secondary medians of the triangle of mixing with two T-S curves in the manner indicated in Fig. 9, and determine the angles formed by tangents with axis s. Evidently this method, like that of Jacobsen, is valid only in the case of mixing of three water masses.

The theory of T-S curves described above has an interesting hydrodynamic interpretation. Indeed, if we consider a two-dimensional horizontal flow of a viscous incompressible liquid in the absence of external forces, the equations of such motion, as known, will have the following aspect:

$$\frac{\partial u}{\partial t} = v\frac{\partial^2 u}{\partial z^2}; \quad \frac{\partial v}{\partial t} = v\frac{\partial^2 v}{\partial z^2}$$

formally analogous to equations (1).

In this system of equations, u and v are components of the horizontal vector of velocity along the rectangular axes of coordinates x and y, respectively. It is easy to understand that in this case of motion of a liquid the hodograph of velocities presents an analogy to the T-S

curve, while the apices of the triangle of mixing are the ends of the three vectors, corresponding to the initial distribution of velocities in the layers of moving liquid.

Thus, in the case considered, the hodographs of velocities possess all the geometrical properties of T-S curves and with the help of formulas (21) and (26) it is possible to determine the value of the kinematic coefficient of viscosity.

A generalization of the theory of T-S curves applicable to any finite number of intermediate layers in the sea is now being prepared.

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PECULIARITIES OF DIURNAL VERTICAL MIGRATIONS OF ZOOPLANKTON IN POLAR SEAS[1]

By

B. G. BOGOROV

Laboratory of Oceanology, Academy of Sciences, U. S. S. R.

Studies of diurnal vertical migration in the polar seas are of special interest since we are able to make observations in nature (without the possible drawbacks of laboratory experiments) of the behavior of animals under the widely varying light conditions that prevail during different seasons. Thus, during the polar summer it is possible to investigate the diurnal migration under conditions of uninterrupted daylight, during the polar autumn and spring under changing conditions of alternating days and nights, and finally in winter under conditions of permanent darkness. At present a series of special diurnal stations are available, taken mainly in the Barents Sea, as well as in the White Sea. Unfortunately, owing to weather conditions, no diurnal stations have been obtained as yet in winter and spring.

I. VERTICAL MIGRATIONS OF ZOOPLANKTON UNDER CONDITIONS OF PERMANENT DAYLIGHT (IN SUMMER)

We have a series of diurnal stations taken in the Barents Sea (Bogorov, 1938) and the White Sea (Bogorov, 1941) in summer, as well as unpublished data. The organisms investigated were: *Calanus finmarchicus, Pseudocalanus elongatus, Microcalanus pygmaeus, Metridia longa, Metridia lucens, Acartia longiremis, Oithona similis, Harpacticus superflexus, Sagitta elegans, Oikopleura vanhöffeni*, and larvae of bottom animals; the investigations included adults as well as young stages of development.

The results showed that all the dominant species perform no such regular shiftings during a 24-hour period as are characteristic of more southern latitudes (Esterly, 1911, 1912; Russell, 1925–26–27; Clarke, 1933, 1936, *et al.*). It is known, due to the general occurrence of this phenomenon, that the diurnal vertical migration of plankton is considered one of the essential manifestations of the life activity of plankton affecting the whole biological regime of the sea, both predators and prey (Bogorov, 1939a, b).

[1] Proofs not seen by author.

Even such species as *Calanus finmarchicus* and *Sagitta elegans*, under conditions of diurnal daylight in the Barents Sea in summer, maintain an almost unchanged vertical distribution through the 24-hour period. As already stated (Bogorov, 1938), this almost invariable diurnal vertical distribution is not achieved passively with the organisms merely remaining in the water level selected, but rather it is achieved by active swimming, since the tidal phenomena in the open sea (Zubov, 1932) cause considerable shifting of water particles up and down, which water movement has to be overcome by the organisms. Thus, in the Barents Sea during summer, under conditions of permanent daylight, a) the organisms tend to occupy a definite habitat level with optimum illumination, and b) tidal phenomena force the animals to move constantly upwards and downwards in order to overcome displacement by the movement of water particles and to maintain their habitat level.

The study of this phenomenon in the more southern White Sea is of particular interest. Here, although the surface of the sea is permanently illuminated in summer, the sun lies low on the horizon during the night, so that conditions of light penetration into the water are less favorable and the period of feeble water illumination lengthened.

Investigations of a series of organisms showed that most species maintain an almost constant vertical distribution during the 24 hours. In the White Sea, in the region investigated, only the surface layer is considerably affected by tidal phenomena. Therefore, only the inhabitants of this layer have to perform diurnal vertical migrations of the polar type (such as in the Barents Sea), whereas animals living in deep water layers need no extensive, active migrations to maintain their optimum habitat level.

In contrast with the Barents Sea, in the White Sea the usual type of diurnal vertical migration of plankton also was observed. Thus, for instance, *Metridia longa* is to be found in the surface layers in greater quantities in the evening and night hours than in the daytime. Furthermore, although the vertical distribution of the total quantity of plankton does not vary considerably during the 24 hours, the quantity found in the upper layer is greater in the evening and night than in the morning and afternoon. Therefore, we are here in the presence of a diurnal vertical migration of plankton of the usual (southern) type. Although of not such large magnitude as in more southern seas, its occurrence in the White Sea in the summer emphasizes once more the role of light in the phenomenon of diurnal migration.

II. THE VERTICAL MIGRATION OF ZOOPLANKTON UNDER CONDITIONS OF ALTERNATING DAY AND NIGHT (IN AUTUMN)

What is the behavior of organisms during the period of alternating day and night? If they perform regular diurnal migrations of the usual type during this period, then the role of light in this phenomenon becomes still more evident.

During our observations of the variations in the quantity of zooplankton in the surface layers of the Kara Sea (Table I) in 1934, we

TABLE I. Biomass of Surface Zooplankton and Number of Organisms of Some Species (per 1 m³) in Night and Day hauls Taken in the Southeastern Barents Sea and Western Kara Sea in September, 1940

	Biomass of zooplankton per 1 m³ (in mgs)	*Calanus finmarchicus*	*Pseudocalanus elongatus*	*Acartia*	*Oithona*
Night	200	45	450	210	1500
Day	115	5	370	660	4500

	Temora	*Microcalanus*	*Appendicularia*	Eupheusidae[2]	Polychaeta	Trochophora
Night	410	3100	170	1	74	60
Day	30	2400	2	—	10	1

found that the biomass of zooplankton was greater in the evening and night hauls than in the day hauls. This was due to the fact that several species (*Calanus finmarchicus*, *Fritillaria borealis*, Polychaeta juv., Euphausiidae, and others) occurred chiefly in night hauls. So this is undoubtedly evidence of diurnal vertical migration.

Chmysnikova (1937), in working out the zooplankton material collected in Vilkitsky Strait in September, observed that several species (*Calanus finmarchicus*, *Pseudocalanus elongatus*, *Fritillaria borealis*, and *Sagitta elegans*) occur more often in night hauls than in day hauls. In spite of the fact that this material was not collected on special stations, and moreover, was not treated by any precise quantitative method, the results obtained by Chmysnikova convincingly confirm the occurrence of a diurnal vertical migration of polar zooplankton during the period of alternating day and night.

To obtain a final solution of this problem, we worked out the special four diurnal stations taken in the Barents Sea in October, which was quite an achievement considering the weather conditions prevalent in autumn. As a result, it was established that almost all dominant species perform regular diurnal vertical migrations. During the

[2] The author's spelling is given here, although it is possible that he intended Euphausiidae. Editor.

night great masses of plankton concentrate in the upper layers, whereas in the daytime they sink into the deep waters. This is well illustrated by station no. 4687.

A. The dominant species found on this diurnal station were:

1. *Calanus finmarchicus*	st. IV, V, and VI
2. *Metridia longa*	st. IV, V, and VI
3. *Metridia lucens*	st. IV, V, and VI
4. *Microcalanus pusillus*	st. VI
5. *Pseudocalanus elongatus*	st. IV, V, and VI.

These undertake regular diurnal migrations in the Barents Sea under conditions of polar autumn, with alternating day and night. Each of these species has its peculiarities, but common to all of them is their aggregation in huge quantities in the upper layer 50–0 m. (Table II),

TABLE II. Percentage Distribution of Organisms of the Dominant Species at Station 4687. Hauls Taken During the 24 Hours Are Divided into Two Periods: Dark, from 6 P. M. to 5 A. M., and Light, from 6 A. M. to 6 P. M. Moreover, All the Hauls Are Grouped into Surface (50–0 m.) and Deep (200–50 m.) Water

Stages	Depth (m.)	*Calanus finmarchicus*		*Metridia longa*		*Metridia lucens*		*Pseudocalanus elongatus*	
		6 p. m. to 5 a. m.	6 a. m. to 6 p. m.	6 p. m. to 5 a. m.	6 a. m. to 6 p. m.	6 p. m. to 5 a. m.	6 a. m. to 6 p. m.	6 p. m. to 5 a. m.	6 a. m. to 6 p. m
IV	50–0	63	4	43	12	80	1	39	10
	200–50	37	96	57	88	20	99	61	90
V	50–0	77	1	29	25	85	2	45	6
	200–50	23	99	71	75	15	98	55	94
VI ♀	50–0	92	—	36	—	95	2	73	21
	200–50	8	100	64	100	5	98	27	79

All Stages	Depth (m.)	*Microcalanus pygmaeus*		*Acartia longiremis*		*Oithona similis*		*Oithona plumifera*	
		6 p. m. to 5 a. m.	6 a. m. to 6 p. m.	6 p. m. to 5 a. m.	6 a. m. to 6 p. m.	6 p. m. to 5 a. m.	6 a. m. to 6 p. m.	6 p. m. to 5 a. m.	6 a. m. to 6 p. m.
	50–0	78	25	70	20	86	80	23	40
	200–50	22	75	30	80	20	20	77	60

often even in the layer 10–0 m. in the hours of darkness. In the daytime, on the contrary, the bulk of the organisms remain in the deep water layers, some of the species descending in the deepest layers of 200–100 and 150–100 m.

A. Not only is the limited diurnal vertical migration characteristic of adults and older stages of development but also of the younger stages of the species mentioned. However, as young stages are scarce at this time of the year they cannot be discussed in detail.

B. Some representatives of the krill always occur in samples in single specimens (a drawback of Nansen's net); however, they are found more often in the upper layers in the hours of darkness and in deep water layers in the daytime.

C. Two dominant species, *Oithona similis* and *O. plumifera*, perform no diurnal vertical migrations even under conditions of alternating day and night.

D. Consequently, the diurnal vertical migrations of plankton in the Barents Sea, under conditions of alternating day and night, are similar to such migrations in all southern seas where this phenomenon, due to its general occurrence, affects the biology (especially the vertical distribution during the 24 hours) of herring and other plankton-eating fishes.

The diurnal migrations of plankton here described are not related to the vertical shifting of water particles during the 24 hours. Hydrographic data show that at these stations the shifting of water particles is very limited, if there is any shifting at all. At different moments of the 24-hour period the temperature distribution at different levels (horizons) remains almost unchanged.

Finally, we may describe the scheme of diurnal vertical migration of zooplankton at different latitudes as follows (Fig. 10).

1. In seas of moderate and southern latitudes, with a permanent regular alternation of day and night, the diurnal migration is of the usual, universal type (Fig. 10B); *i. e.*, once during the 24 hours, with the beginning of twilight, the migrating animals swim upwards, ascending from great depths (often as deep as 500 m.) to the upper layers. At dawn they begin to swim downwards, sinking in the daytime into the deep water layers. During these migrations, which exceed even ½ km., the animals swim through water layers which have quite different physical conditions, seeking in the daytime to avoid unfavorable light conditions, and, in the evening, to reach the upper layers rich in food.

2. In polar seas the diurnal vertical migration is subject to great seasonal changes. Thus in summer (Fig. 10A), under conditions of permanent daylight, the animals maintain an almost invariable vertical distribution, actively or passively (depending on the behavior of water particles) keeping to their habitat level. Since the water particles, under the influence of tidal phenomena, shift twice upwards and twice downwards during the 24-hour period, the animals which remain all the time in one horizon are subject to quite different physico-chemical conditions. They submit to these changes in order to maintain themselves at the level with optimum light conditions.

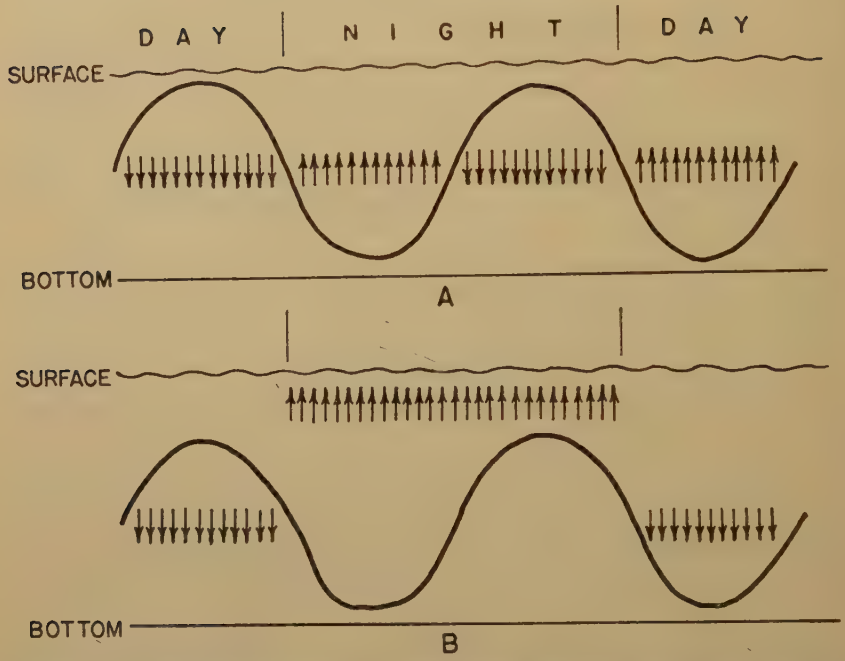

Figure 10. Diagrammatic patterns of diurnal vertical migration under Polar conditions (A) in summer during 24 hours of daylight, and (B) in autumn under conditions of alternating nights and days.

In the more southern White Sea some species exhibit a diurnal vertical migration of the usual type, while others have a more constant distribution which is typical of polar seas. This is explained by the fact that the White Sea is a transition zone in which, although daylight is permanent in summer, the sun lies so near the horizon at night that almost no rays penetrate into the water.

3. In the autumn in the polar seas the days alternate with nights. As a result, the same species and possibly even the same organisms which maintained an invariable vertical distribution during the 24 hours of summer daylight begin to perform migrations of the usual type (Fig. 10B). They swim towards the surface in the dark and downwards in the daytime, passing through water layers with quite different conditions. These data give conclusive evidence of the role of light in the phenomenon of diurnal migration and the importance of this factor for the vertical distribution of plankton.

4. Consequently, the study of the vertical distribution of plankton has a general bearing. It is impossible to assign any species or any age-group to a definite water layer or to definite physico-chemical

conditions without a knowledge of the diurnal vertical migration of the particular group. Since diurnal vertical migrations are characteristic of most zooplankton species (Clarke, 1933, 1934a, b; Gardiner, 1933; Esterly, 1911: Russell, 1927; Rose, 1925, *et al.*), this being a phenomenon of normal life activity during their partial or entire individual life, we can judge the ecological conditions characteristic of a given species only in the light of the phenomenon of vertical plankton migrations. Thus we have to consider all the water layers in which the organisms dwell during the 24 hours as forming the ecological conditions characteristic of the given species.

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PHYTOPLANKTON-ZOOPLANKTON RELATIONSHIPS ON GEORGES BANK[1]

By

GORDON A. RILEY and DEAN F. BUMPUS

Woods Hole Oceanographic Institution
and
Bingham Oceanographic Laboratory

INTRODUCTION

Comparisons of different oceanic regions often suggest that in the largest sense there is a direct relationship between phytoplankton and zooplankton—that is, banks and coastal areas with large concentrations of phytoplankton are likely to be rich in zooplankton, while sparser crops of both occur in deep oceanic waters. On the other hand, surveys of particular areas often show an inverse relationship, with local swarms of zooplankton occurring in phytoplankton-poor waters, alternating with dense patches of phytoplankton containing few animals. Harvey, Cooper, LeBour and Russell (1935) explained the inverse relationship observed in the English Channel as a grazing phenomenon, while Hardy and Gunther (1935) advanced the theory of animal exclusion, which postulated avoidance of phytoplankton patches by the animals. Steemann Nielsen (1937) and Clarke (1939) elaborated the theory of the grazing phenomenon with particular emphasis on the time factor, pointing out that the presence of a swarm of adult copepods is the result of weeks of growth and is dependent on the quantity of phytoplankton available throughout the growth period. Thus, as described by Marshall, Nicholls and Orr (1934), it is possible for such a swarm to pass successfully through its developmental stages at the same time as (and possibly as a direct result of) a diatom flowering. In such a case two relationships between phytoplankton and zooplankton might be described: (1) a direct correlation between a diatom flowering and the swarm of copepods to which it eventually gives rise, and (2) an inverse relation obtained by comparing an area in which the zooplankton eventually grazes the phytoplankton to a low level with other localities in which this has not occurred.

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OBSERVATIONS ON GEORGES BANK

Fig. 11A shows the mean total phytoplankton and zooplankton populations of Georges Bank as determined during cruises made in 1939 and 1940 (Clarke, Pierce and Bumpus, 1943; Riley, 1941). The seasonal cycles are similar to those in numerous other localities, with spring phytoplankton and summer zooplankton maxima, mid-winter minima for both, and a gradual upward trend in the zooplankton population during the development of the spring diatom flowering; these are followed by a sharp increase in the number of animals in late April and early May, coincident with the decline of the diatom burst. Thus the seasonal trend in the phytoplankton-zooplankton relationship is direct in the early spring and inverse later.

Analysis of individual station records reveals that the horizontal distribution of plant and animal plankton varied from one month to the next in a way that reflected the general seasonal trend. During March, areas in which the spring diatom flowering was beginning were also foci of zooplankton increase. In May, on the other hand, there was little zooplankton in areas of diatom abundance, the latter being sparse in places where zooplankton growth had attained large proportions. Correlations were prepared showing the relationship between the horizontal distribution of phytoplankton and zooplankton on each of the cruises. These are plotted in Fig. 11B. They show clearly the moderately high direct relationship in March and the highly significant inverse relation in May. During the other cruises the correlations were statistically insignificant.

Further facts of interest in this connection are revealed by examination of the seasonal cycles and horizontal distribution of individual species and genera of zooplankton. Fig. 12 shows the cycles of eight of the more important groups and their correlations with total phytoplankton. Seasonal minima were generally accompanied by zero or positive correlations, and in most cases there was a positive correlation at the time when the species was beginning to increase. In each case there was a negative correlation with phytoplankton at the time when the species reached its seasonal peak. All these correlations were either statistically significant or significantly different from the preceding positive correlation, except in the case of Centropages, for which no preceding data are available. Animals such as decapod nauplii and *Pseudocalanus minutus*, which developed a peak population slowly, also showed a slowly declining correlation with phytoplankton, while in other groups both changes were more rapid. Thus, it is evident that individual zooplankton groups showed relationships with phytoplankton in their horizontal distribution that were similar to

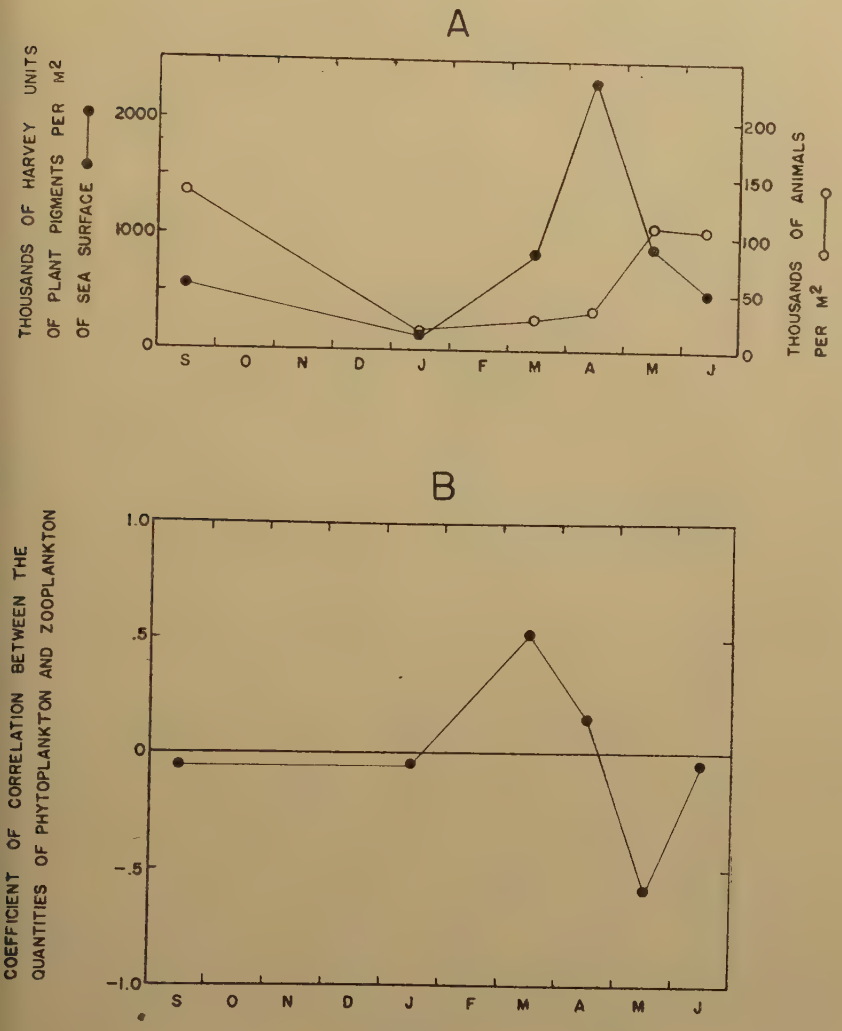
A
THOUSANDS OF HARVEY UNITS OF PLANT PIGMENTS PER M2 OF SEA SURFACE
2000
1000
0
200
150
100
50
0
THOUSANDS OF ANIMALS PER M2
S O N D J F M A M J
B
COEFFICIENT OF CORRELATION BETWEEN THE QUANTITIES OF PHYTOPLANKTON AND ZOOPLANKTON
1.0
.5
0
-.5
-1.0
S O N D J F M A M J

Figure 11.

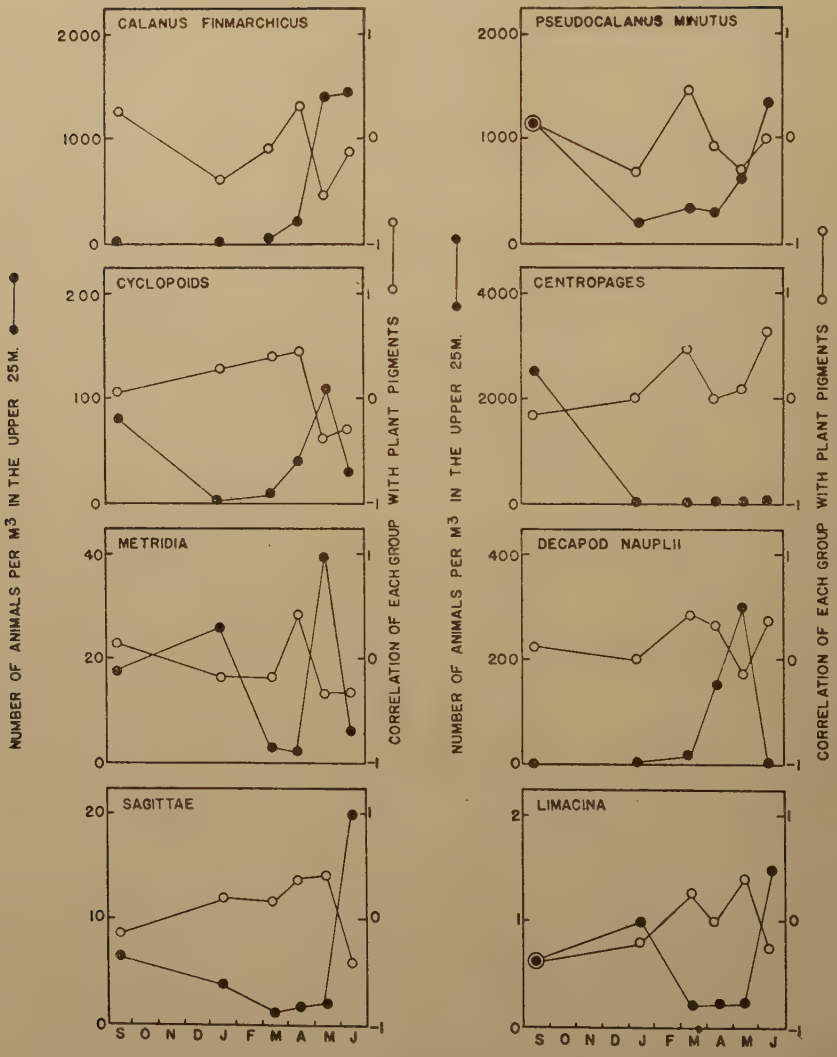
CALANUS FINMARCHICUS
PSEUDOCALANUS MINUTUS
CYCLOPOIDS
CENTROPAGES
METRIDIA
DECAPOD NAUPLII
SAGITTAE
LIMACINA
NUMBER OF ANIMALS PER M3 IN THE UPPER 25M.
CORRELATION OF EACH GROUP WITH PLANT PIGMENTS
S O N D J F M A M J

Figure 12.

those of the total population, and this is particularly significant in that their seasonal peaks appeared at different seasons of the year.

In any problem as complex as plankton relationships there may be some doubt as to the significance of a simple correlation between two groups of organisms, because obviously many other factors can affect their relationship. For example, it is not impossible that variations in temperature might affect both plants and animals in such a way as to produce a significant phytoplankton-zooplankton correlation. Such a situation could be detected, however, by calculating the partial correlation between phytoplankton and zooplankton in respect to temperature.

The statistical method of partial correlations makes allowance for indirect relationships by correcting the correlation between the two main variables on the basis of their relation with the third variable, which is suspected of indirect influence. By an elaboration of the method it is possible to eliminate simultaneously the effects of a number of indirect factors. The only limitation of the technique is the practical difficulty that in such a complex system as the natural environment it is hardly possible to obtain measurements of all the factors that might be important. Therefore such an analysis is only an approximation to the true relationship.

In the present analysis the two factors most likely to have indirect influence are temperature and depth, the latter because stations were made on various parts of the Bank, some of which extended into fairly deep water at its edge, and because important relationships had been noted previously between the depth of water and both the quantity of plankton and the distribution of species. Therefore, these two factors were taken into account in deriving the partial correlations, together with phosphate and nitrate content of the water, which might conceivably have indirect effects. The resulting partial correlation was $-.510$ in May, which was nearly the same as the simple correlation. The correlations for September, January, and June were changed slightly ($-.170$, $.089$, and $-.200$ respectively). The positive correlation observed in March was reduced to an insignificantly low level ($-.015$), and the slight positive April correlation was changed to a somewhat stronger negative one ($-.246$). Thus the direct relation between phytoplankton and zooplankton in the early spring can be explained as the product of other factors of the environment, but there is nothing in the available data that denies the biological significance of the negative correlation observed in May.

DISCUSSION

Negative Phytoplankton-Zooplankton Correlation and Grazing Effect. It is apparent that the plant-animal relationship on Georges Bank is similar to that observed in many other regions in the springtime and therefore might be described as a grazing or animal exclusion phenomenon. There are two reasons, however, for believing that the latter cannot be applied in this particular case. First, the vertical distribution of phytoplankton on Georges Bank was too nearly constant to favor the method of avoidance by vertical migration postulated by Hardy. Second, the time of greatest negative correlation varied from one species to another. It apparently had nothing to do with the richness of the phytoplankton crop which supposedly sets up the avoidance reaction. Rather, the negative correlation, both in total zooplankton and in individual species, was greatest when the zooplankton reached its peak, irrespective of the quantity of phytoplankton in the water at that time. This points to the grazing phenomenon as the cause of the relationship.

The quantitative aspects of the relationship are further elaborated in Tables I and II. The first two columns of Table I show the average

TABLE I. Mean Quantities of Plankton on Georges Bank and Estimates of the Grazing Phenomenon

Month	*Mean plant pigments*	*Mean number of animals per m²*	*Estimate of plant pigment consumption per 1000 animals*	*Estimated total consumption*	*Mean phytoplankton crop and grazing estimate*
Sept.	560	135,000	0.26	35	595
Jan.	120	14,000	−0.47	−7	113
Mar.	830	24,000	0.62	15	845
Apr.	2,300	32,000	5.3	170	2,470
May	870	106,000	3.5	371	1,241
June	480	103,000	0.55	56	536

values for phytoplankton and zooplankton during each cruise. The values for phytoplankton were determined according to the Harvey plant-pigment method and are listed as thousands of "Harvey units" per m². The partial correlations are used to calculate regression equations for the phytoplankton-zooplankton relationship. By this means a quantitative estimate of grazing is derived from the observed negative correlations, and the constants for the regression equations are listed in the third column in terms of phytoplankton (Harvey units x 1000) consumed per 1000 animals. The product of the constants and the mean quantity of animals is an estimate of the total amount of grazing during the time required to develop the correlation,

and this is shown in column 4. The sum of columns 1 and 4 suggests what the phytoplankton would be if no animals were present.

The relationship between phytoplankton and zooplankton can be understood more clearly if an attempt is made to convert the estimates into directly comparable terms. This is done in Table II. Figures

TABLE II. Quantitative Comparisons of Phytoplankton and Zooplankton

Month	*Zooplankton volume cc/m²*	*Dry weight of zooplankton g/m²*	*Dry weight of phytoplankton g/m²*	*Estimated total consumption g/m²*	*Per cent of phytoplankton crop consumed*	*Food requirement, % of zooplankton weight*
Sept.	38.1	9.5	19.6	1.2	6	13
Jan.	11.1	2.8	4.2	−0.2	−5	−7
Mar.	58.2	14.5	29.0	0.5	2	3
Apr.	81.3	20.3	80.5	6.0	7	30
May	152.6	38.1	30.4	13.0	43	34
June	60.1	15.0	16.8	2.0	12	13

for zooplankton volume (column 1) were determined by the displacement method. The second column was derived on the assumption that the dry weight of organic matter in the zooplankton averages 25% of the volume in cubic centimeters. The phytoplankton figures in the third column are based on measurements from a previous paper (Riley, 1941) which gave a conversion factor of 35 mgs. of dry organic matter per thousand units of plant pigments. The fourth column utilizes the same factor together with data from Table I to determine the weight of phytoplankton consumed during the course of development of the observed correlation between phytoplankton and zooplankton. Finally, the last two columns list the data on consumption as percentages of the plant and animal weights.

The gradual development of the negative correlation during the spring months might suggest a static situation in which a swarm of zooplankton developed in a particular local water mass and gradually reduced the phytoplankton crop during a period of two or three months. However, reference to Table II indicates that this is very unlikely since the increment in the weight of zooplankton during the spring months exceeded the estimated total consumption. Moreover, the values in the last column of Table II for April and May are of the same order of magnitude as the estimate made by Harvey and his associates (1935) for one day's consumption at the height of the diatom flowering, while the estimates for other months are similar to the minimum requirements for one day determined by Marshall, Nicholls and Orr (1935) from a study of the respiration of *Calanus finmarchicus*.

In this connection it can be seen in Table II that between the April and May cruises, when the zooplankton was increasing most rapidly,

the mean phytoplankton crop decreased about 50 g. per m², although experiments on Georges Bank plankton (Riley, 1941) showed that the photosynthetic rate was increasing rather than decreasing during this period. The total difference between the experimentally estimated phytoplankton production and the observed crop was about 80 g. per m², most of which probably was due to grazing, although perhaps some of it can be ascribed to death by other causes. Therefore, the total consumption may have been more than ten times as great as the increase in the phytoplankton-zooplankton correlation during the same period would indicate. Thus it is desirable to attempt to evaluate the grazing rate more carefully by considering all the factors involved and by trying to decide whether there is good reason for the discrepancy that appears to exist.

Other Factors Involved in the Grazing Phenomenon. The maximum grazing rate can be estimated by methods similar to those described by Fleming (1939), who suggested the equation

$$\frac{\Delta P}{\Delta t} = P\,[a - (b + ct)], \tag{1}$$

in which the change in the diatom population in respect to time is dependent on a, the rate of multiplication of the population, b, the initial grazing rate, and c, the change in the grazing rate due to changes in zooplankton population. The validity of the equation depends on the assumptions that the rate of multiplication of phytoplankton is constant, that an animal grazes a fixed proportion of the diatoms (filters a unit volume of water) per day, that there is no loss other than by grazing, and that the effects of turbulent mixing are negligible. The equation can be applied to the present study by introducing a term a_1, which represents the change in the multiplication rate with time, which is required according to the evidence from experiments on the photosynthesis of diatom populations on Georges Bank. The resulting equation is

$$\frac{\Delta P}{\Delta t} = a + a_1 t - (b + ct), \tag{2}$$

and integrating,

$$P_t = P_o e^{t[a + \frac{1}{2} a_1 t - (b + \frac{1}{2} c)]}, \tag{3}$$

in which P_o is the initial population, and P_t is the population at time t. Using the equation to express the change in phytoplankton between the April and May cruises, with the experiments on photosynthesis as the basis for estimates of a and a_1, and with c expressed in terms of the change in zooplankton population,

$$\ln 870 - \ln 2300 = 20\ (.023) + 200\ (.0065) - 20b - 200\ (.115b)$$
$$b = .064.$$

Thus, it is estimated that the April grazing rate was 6.4% of the phytoplankton population per day, or 25% of the weight of zooplankton. In May the consumption can be shown to be 17% of the animals' weight per day. These figures are very dependent on the assumption that there was no loss of phytoplankton by any cause other than grazing. Harvey and his associates (1935) believed that in the English Channel loss of diatoms by sinking or natural death was negligible. It is not yet certain whether this conclusion is also applicable to Georges Bank. Therefore the calculated values should be regarded as maximum estimates of grazing.

But the various calculations, rough as they may be, do not leave very much doubt that the correlation represents only a part of the grazing phenomenon, and perhaps a relatively small part. Furthermore, the most obvious explanation of the situation is that the continual tendency of grazing to produce such a correlation was inhibited to a greater or lesser degree by turbulent mixing, which tended to redistribute the populations more uniformly.

Georges Bank is an area dominated by strong winds during most of the winter and spring. It has rotary tidal currents typical of offshore banks, which attain a maximum velocity of three or four knots at the surface. Much of the bank water is homogeneous in respect to temperature and salinity, as is shown in diagrams by Clarke, Pierce and Bumpus (1943). However, mixing is seldom rapid or complete enough to destroy completely the last vestiges of vertical stratification of biologically active materials (Riley, 1941). With this general picture of the hydrography of the bank, it is to be expected that there might be enough turbulent mixing to interfere with the development of plankton patchiness due to grazing.

Therefore, the examination of the data with the idea of determining how mixing would affect the distribution of the plant and animal populations is in order. In the first place it is clear that although mixing tends to level the populations, growth by geometrical progression has the opposite effect. For example, during the rapid period of increase of animals between April and May, the average population rose from 24 to 106 thousand animals per m^2, a growth rate of 5.9% per day. In April 70 thousand animals was a moderately large population (the mean plus the standard deviation). If this latter population increased at the same rate, it would number 232 thousand in May. Obviously this is a much larger numerical difference between the large and average populations, although the ratio

remains constant. Actually, however, in May 183 thousand animals was a large population, judged by the same criteria. In other words, there was a large numerical increase but a reduction in the ratio. Moreover, this reduction in the ratio can be used as an index of dilution of the population by mixing, provided the growth rates were relatively uniform. According to the figures given above, mixing caused a rate of reduction of the percentage difference between a large and an average population of 2.4% per day.

Studying the effect of mixing on the diatom population is more complicated because of the number of factors involved. It is necessary to use an equation of type (3) as a basis and to elaborate it by introducing factors representing the change caused by mixing. Thus in the equation

$$P_t = P_o e^{[t(a-b)+\frac{1}{2}t^2(a_1-c)]\,[1-t\,(d+\frac{1}{2}d_1 t)]}, \qquad (4)$$

d is the initial rate of dilution of the population by mixing, and d_1 is the change in the rate with time. This is not quite the same as the procedure described for zooplankton mixing rates, but it can easily be transformed into comparable terms.

In dealing with a population of average size, it is assumed that d and d_1 are negligibly small. They have a finite value when the population is larger or smaller than average. A moderately large population, defined as the mean plus the standard deviation, was 3120 thousands of units of plant pigments in April and 1393 in May. Because of the negative phytoplankton-zooplankton correlation, the larger plant populations were accompanied by smaller animal populations, the number as determined by the regression equations being 23 thousand per m² in April and 67 thousand in May. It is assumed that the initial grazing rate was correspondingly less than the value previously determined for the average population, or $b = 23/32 \times .064 = .046$. It is also assumed that the grazing rate increased proportionally to the increase in population; that is, $c = (67 - 23)\ b/23t = .096b$. Then

$$ln\ 1393 - ln\ 3120 = \{20\,(.023 - .046) + 200\,[.0065 - .096\,(.046)]\}\,\{(1 - 20\,(d + 10d_1)\}\ d + 10d_1 = .082.$$

Thus the average rate of dilution of a moderately large plant population by mixing was 8.2% per day during the April–May period. In order to compare this figure with the previously determined rate of dilution of zooplankton by mixing, it is necessary to determine the ratio between the large and average populations, reduce it by the amount indicated for zooplankton mixing, and transcribe this figure back into terms of plant pigments. When this is done, the calculated values of d and d_1, based on the zooplankton dilution rate, are 0.0022 and 0.00014 re-

spectively. It is apparent that there is a wide discrepancy in the two estimates. The rate of mixing of phytoplankton populations appears to be 23 times as great as that of zooplankton.

The calculations suggest alternative conclusions. (1) The importance of the grazing phenomenon may be exaggerated. If part of the decrease in phytoplankton were caused by other factors, the estimate of mixing would be altered. (2) There may actually be more or less difference in the rate of mixing of plant and animal populations. Such a difference could occur only by partial segregation of the populations, but diurnal migration provides a means by which this might be effected. The alternative conclusions will be examined in turn, although, as will be seen, it is speculatory to attempt to choose between them.

Grazing Effect versus Loss of Phytoplankton by Natural Death. Experiments with laboratory cultures of diatoms (Riley, 1943) showed that after the development of a maximum population there followed a period of decrease which appeared to be a logarithmic function of the number of cells in the culture, and which appeared to be initiated by exhaustion of available nutrients. During this period of rapid natural death a large part of the population looked debilitated and was in a state of depressed physiological activity as evidenced by a low photosynthetic rate.

Comparison of these results with the natural plankton associations of Georges Bank revealed some similarities and some differences. Many of the May diatoms appeared senile, yet the photosynthetic rate was higher than in April. Counts made on individual species after three or four days' growth in experimental bottles showed increases in some species and decreases in others. It seemed likely that each species went through a growth cycle somewhat similar to that of laboratory cultures but at different times, so that at no time was the whole plankton association in a state of decay. Nor was there any time when such nutrients as phosphate or nitrate approached exhaustion.

It seems likely therefore, that a certain amount, although probably not a major part, of the decrease in population previously ascribed to grazing was actually caused by natural death. In attempting to establish its quantitative aspects it seems reasonable to assume that the death rate was a logarithmic function of the population, as in the case of laboratory cultures. Therefore, as the simplest example of such a relationship a factor s will be introduced into equation (4), which represents the death of a fixed percentage of the population each day. At the same time it will be assumed that the rate of dilution of

the phytoplankton by mixing is the same as that previously determined for zooplankton. The values for d and d_1 are, as previously stated, .0022 and .00014 respectively. Then in respect to the average population, which is not affected by mixing,

$$ln\,870 - ln\,2300 = 20\,(.023) + 200\,(.0065) - 20b - 200\,(.115b) - 20s$$
$$43b + 20s = 2.731.$$

A large population, as previously defined, takes the form

$$ln1393 - ln\,3120 = [20\,(.023) + 200\,(.0065) - 20\,b_1 - 200\,(.096b_1) - 20s]\,[1 - 20\,(.0022) - 200\,(.0014)]$$

$$39b_1 + 20s = 2.633.$$

The term b_1 in the second equation points out the fact that the grazing rates of the two populations differ by the ratios of the populations, or 32 : 23; therefore the equation may be rewritten $28b + 20s = 2.633$. Subtracting this from the equation for the average population, $b = .0065$. Thus the grazing rate in April is estimated to be about 0.5% of the diatoms per day, or 2.5% of the weight of the zooplankton. This is less than the increase in the weight of the zooplankton crop, and is therefore impossibly small. If the death rate were not constant, but accelerated or decelerated with time, it would not make any difference in the apparent value of the grazing rate. The latter would be changed only if the death rate of the large population were different from that of the average population. This seems unlikely, although there is no definite evidence on the subject. Lacking such evidence, any conclusion is speculatory. However, it seems rather likely that while some small part of the observed decrease in phytoplankton may be ascribed to natural death, no reasonable assumption about the death rate can avoid the necessity of postulating also a phytoplankton mixing rate larger than that of the zooplankton.

Diurnal Migration and Grazing. The currents on Georges Bank are of two kinds: rotary tidal currents and a residual drift. In either case the frictional effect of the bottom is such that the currents are expected to have their greatest velocity near the surface. In the case of tidal currents, not only does the velocity generally diminish toward the bottom, but also the direction of the current deviates toward the right. This is described in a paper by Sverdrup (1927). Therefore the plankton at any particular depth has a different history of past movements from the plankton above and below, and if the plankton patches are sufficiently small, it also has a different history of past associations with other populations. This, combined with vertical turbulence, facilitates the mixing of populations. The mixing

effect, moreover, will be more pronounced in the case of phytoplankton, which is passively scattered through the entire water column, but less in zooplankton, which tends by vertical migration to swarm at a particular depth range and therefore to be transported by horizontal currents that are more nearly uniform in velocity and direction. Thus it is possible to conceive that zooplankton swarms might be scattered less than the diatoms by turbulent mixing, and also that the association of a group of animals with any one phytoplankton population might be relatively transitory.

This would adequately explain the evidence that the observed negative correlation between plants and animals represents only part of the total grazing effect. It might be noted also that the theory resembles Hardy's theory of animal exclusion insofar as it postulates that diurnal migration is an essential part of the plant-animal relationship. Like his hypothesis, it is applicable in any place where, within the depth range of diurnal migration, current velocity varies with depth. There the resemblance ends, since the negative correlation is postulated as a result of transitory but intensive grazing of any population encountered at random rather than an avoidance of dense patches of phytoplankton.

Unfortunately, however, the theory must remain in qualitative terms for the present. More complete data on both the currents of Georges Bank and the horizontal distribution of plankton will be required before it will be possible to attempt a final solution of grazing, mixing, and phytoplankton death rates. Further work is also required to test some of the assumptions on which the equations are based, which, although they appear reasonable at the moment, are not necessarily true. It does not seem inappropriate, however, to approach the subject in this way if by doing so the unsolved problems of plankton biology can be stated more clearly.

SUMMARY

1. There is a significant inverse relationship between the horizontal distribution of Georges Bank phytoplankton and zooplankton at the time when the latter is increasing most rapidly. This is true not only of the total zooplankton but also of several individual species and genera that were examined. The evidence points to grazing as the cause of the inverse relationship.

2. Quantitative estimates of the amount of grazing required to develop the observed negative correlation between plant and animals are of the order of 35% of the weight of the animals in May, when the most rapid increase in the animal population occurred. This, however,

did not represent the total amount of grazing that occurred during the spring period, because the increase in weight of the zooplankton was considerably larger. It is suggested that turbulent mixing tended to redistribute the populations so that the correlation was not as fully developed as it would be otherwise.

3. An attempt is made on theoretical grounds to determine rates of grazing. The maximum amount of grazing that could occur (judged by the difference between the phytoplankton production rate and the rate of change of the standing crop) was about 25% of the animals' weight per day in April and 17% in May.

4. It is estimated that the effect of turbulent mixing on zooplankton amounted to a daily reduction of about 2.4% of the percentage difference between a given population and the average population. The effect of mixing on phytoplankton appears to be very much greater.

5. The reason for the apparent difference in mixing rates cannot be absolutely established, but it appears likely that diurnal migration is involved. It is reasonable to suppose that on Georges Bank the velocity and direction of the currents vary with depth. In such a case turbulent mixing should be more effective in levelling the phytoplankton populations, which are scattered through the entire water column, than zooplankton, which tends to aggregate at particular depths.

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CORRELATION BETWEEN FLUCTUATIONS IN ABUNDANCE OF THE PACIFIC SARDINE (*SARDINOPS CAERULEA*) AND SALINITY OF THE SEA WATER[1]

By

LIONEL A. WALFORD

Fish and Wildlife Service
United States Department of the Interior

In the course of studying several seasons' statistics on the age composition of the commercial catch of the Pacific sardine (*Sardinops caerulea*)[2] I have found what appears to be a fairly indicative measure of year-class strength in the total number of three-year-old fish[3] caught by commercial fishermen in all Pacific Coast ports of United States and Canada. The fourth year is the youngest age that sardines are fully available to fishermen; at that age they seem to frequent the fishing grounds as consistently as do older fish; they are large enough then to be fully desirable commercially, and fishermen do not try to avoid them as they do smaller and younger fish. Hence, so long as the total fishing effort does not change, the number which a fisherman can catch on the average parallels the total abundance.

For present purposes, it is assumed that total mortality (*i. e.*, from natural causes and from fishing) of one- and two-year-old fish remained essentially constant from year to year during the period 1934 through 1941. It is likewise assumed that the total fishing effort in all ports remained essentially constant during that period. The first of these assumptions permits the utilization in this analysis of three year classes for which data on ages one and two are lacking. The second avoids the necessity of adjusting the catch figures by some measure of fishing intensity. Although the first assumption cannot be tested until the catch histories of several year classes have run their courses, the second is supported by evidence in catch-per-unit-of-effort studies on the sardine fishery (Silliman and Clark, 1945). The com-

[1] Published by permission of the Director of the Fish and Wildlife Service.

[2] Length-frequency data and scales have been collected by five Pacific Coast agencies: United States Fish and Wildlife Service, Department of the Interior; Fisheries Research Board of Canada; California Division of Fish and Game; Fish Commission of Oregon; Department of Fisheries of the State of Washington.

[3] "Three year old" fish are those in the fourth year of life, *i. e.*, they have three annual marks on their scales.

putation of numbers of fish at age three was done from the following data and in the following steps.

1. Total number of fish caught, by ports.[4]
2. Percentage age composition of samples of the catch in each port.[5]
3. Number of fish of each year class caught, by ports. This was obtained by multiplying item 1 by item 2, under the assumption that the samples represent the catch.
4. Number of fish of each year class caught along the entire coast. This was obtained by summing, age by age, the number landed in the several ports as determined in item 3.

TABLE I. Relative Strength of Sardine Year Classes. Total Number of Three-year-old Sardines Caught in United States and Canadian Waters, by Seasons of Capture

Year Class	*Season of Capture**	*Millions of Fish*	*Percentage Deviation from Average*
1934	1937–38	1200†	− 5.0
1935	1938–39	930†	−26.4
1936	1939–40	1316†	+ 4.2
1937	1940–41	1350	+ 6.9
1938	1941–42	1648	+30.5
1939	1942–43	1912	+51.4
1940	1943–44	1028	−18.6
1941	1944–45	721	−42.9
	Average	1263	

* The "fishing season" extends from July (in northern waters) to March 1 in southern California.

† Numbers of 3-year-old fish caught are not available for these year classes. They were estimated from the subsequent catches of those year classes, taking into account the mortalities as indicated by the relative numbers caught in successive years.

In Fig. 13 these data are plotted in a dotted line as percentage deviations from their average (Table I, column 4). Among the numerous environmental phenomena that might be responsible for these anomalies by affecting the early life stages when mortality is thought to be highest and most variable, salinity and temperature are the only ones on which exist data for a long series of years. Of these two, salinity is most closely associated with the nutrient salts, the concentration of which evidently fluctuates widely along the Pacific Coast with fluctuating intensity of upwelling; and the concentration of nutrient salts presumably is correlated with the production of plankton organisms on which sardines feed.

[4] These statistics were given by the California Division of Fish and Game and the Fisheries Research Board of Canada.

[5] Age determination from scale studies was done by the Fish and Wildlife Service and the California Division of Fish and Game.

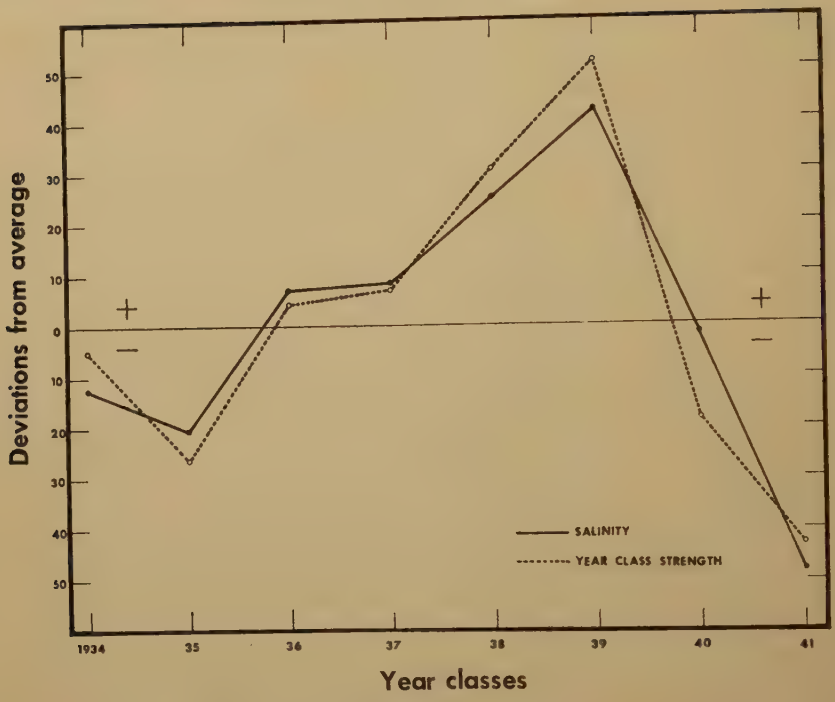

Figure 13.

Since the young crop of sardines is produced in the spring, it is to be expected that any relation between salinity and their survival would be best shown by salinity data collected in the months following that season. It is also to be expected that observations in southern California would be more closely associated with year-class strength than those made at other regions of the Pacific Coast; for according to all available evidence the chief spawning and nursery grounds of the sardine, or at least of that part of the sardine population that is exploited commercially, occurs off southern California.

Accordingly, daily records of surface salinity made at La Jolla, California, were averaged in three- and four-month periods for each of the years in which the eight sardine broods under discussion had been spawned. The coefficients of correlation between these averages and the measures of year-class strength given above are tabulated in Table II. The results conform to expectation. The coefficients are without statistical significance (according to Fisher's t test) *only* for the early months of the calendar year. They are highest for the summer months. This is logical, for in summer the young sardines are still

very young and their demand for food is then most critical. Also, the production of plankton probably profits most from the year's maximum intensity of upwelling, which occurs from March to July (Sverdrup, Johnson and Fleming, 1942).

TABLE II. Coefficients of Correlation (r) Between Average Salinity for Three- and Four-Month Periods and the Strength of Year Broods Produced from 1934 to 1941 Inclusive

3-Month Period Beginning:	r	P*	*4-Month Period Beginning:*	r	P*
Jan.	.382	.1	*Jan.*	.497	.1
Feb.	.500	.1	*Feb.*	.557	.05
Mar.	.523	.1	*Mar.*	.594	.05
Apr.	.708	bet. .02 & .05	*Apr.*	.782	.01
May	.890	.001	*May*	.899	.001
June	.960	.001	*June*	.938	.001
July	.918	.001	*July*	.910	.001
Aug.	.838	.01	*Aug.*	.858	.01
Sept.	.810	.01	*Sept.*	.851	.01
Oct.	.842	.01	*Oct.*	.909	.001
Nov.	.948	.001	*Nov.*	.866	.01
Dec.	.731	.02	*Dec.*	.591	.05

* P is the probability (calculated by Fisher's t test) that as high a correlation or a higher one would occur by chance.

In Fig. 13 the averages of salinity for June, July and August in the eight seasons under discussion (Table III) are plotted in a solid line as percentage deviations from their average. The parallelism between year-class strength and average summer salinities is perfect over the period studied. The coefficient of correlation between the two (r) is .96 with a probability (P) of less than .001 (according to Fisher's t test) that as high a coefficient or a higher one could occur by chance.

TABLE III. Average Surface Salinity Records at La Jolla, California, for June, July and August*

Year	*Aver. Summer Salinity* ‰	*Percentage Deviation from Average* × *10,000*
1934	33.647	−12.5
1935	33.620	−20.5
1936	33.713	+ 7.1
1937	33.717	+ 8.3
1938	33.773	+24.9
1939	33.830	+41.9
1940	33.683	− 1.8
1941	33.527	−48.1
Average	33.689	

* These data were compiled and made available by the Scripps Institution of Oceanography.

This is but another item in the growing body of evidence that fluctuations in the size of year classes of fishes is the consequence of fluctuating infant or adolescent mortality, and that this in turn results from fluctuating environmental conditions. It appears likely that in the sardine one of these conditions may be the abundance of food. This must vary directly with the availability of nutrient salts, the latter with strength of upwelling and this in turn with the force and duration of northwest winds which prevail along the Pacific Coast in summer (Sverdrup, Johnson and Fleming, 1942). Dr. Sverdrup, writing in a letter concerning the manuscript of this paper, has suggested ". . . the strength of upwelling as reflected in the salinity may also modify the currents near the coast such that in years with strong upwelling, the eddies on the shore side of the main flow are better developed. It seems to me that the survival of the sardine larvae must also be related to the type of circulation . . ."

Correlation between year-class strength and physical conditions has been reported for other species; for example, Johansen (1927) found correlation between the number of young plaice fry taken in special hauls and both the surface salinity and the volume of plankton. He wrote (p. 16), ". . . when there is a relatively marked outflow of comparatively fresh water from the Baltic through the Belts and the Southern Kattegat, the tiny plaice larvae fail to obtain sufficient nourishment, and die of starvation *en masse*."

Carruthers and Hodgson (1937) found a striking parallelism in the percentage of 3-year-old herrings in the catches of the East Anglian autumn fishery and the atmospheric pressure gradients controlling run of wind in the southern Bight from the Straits of Dover during the spawning seasons concerned.

TABLE IV. Average Monthly Surface Salinity at Scripps Institution Pier, La Jolla, California, 1934 to 1941 Inclusive* (in parts per mille—33.00)

	'34	'35	'36	'37	'38	'39	'40	'41	'42
Jan.	.54	.40	.51	.40	.70	.48	.72	.32	.31
Feb.	.53	.28	.26	.25	.66	.49	.60	.29	.37
Mar.	.53	.42	.46	.04	.15	.57	.63	.96	.36
Apr.	.61	.51	.58	.37	.66	.61	.58	.84	.41
May	.67	.60	.64	.57	.73	.75	.71	.23	.54
June	.68	.65	.67	.68	.78	.81	.70	.49	.64
July	.68	.62	.75	.72	.79	.86	.64	.56	.64
Aug.	.58	.59	.72	.75	.75	.82	.71	.53	.61
Sept.	.61	.51	.66	.76	.65	.62	.57	.49	.59
Oct.	.52	.50	.45	.67	.56	.68	.52	.35	.63
Nov.	.52	.49	.55	.71	.57	.72	.44	.33	.61
Dec.	.43	.54	.52	.62	.53	.76	.37	.31	.53

* These data were compiled and made available by the Scripps Institution of Oceanography.

SUMMARY

The size of a year class of the Pacific sardine is measured in this study by the number of individuals belonging to that class caught by the commercial fishery during their fourth year of life. This measure, determined for year classes 1934 through 1941, is correlated positively and significantly with average daily summer surface salinity. Judging from the oceanography of the Pacific Coast, it is concluded that the salinity reflects the intensity of upwelling which brings up material nourishing the plankton; and it is suggested that the summer, when the aforesaid relationship is best demonstrable, is the most critical period in the life of the young sardine, when an abundant supply of food is most essential.

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FACTORS CONTROLLING PHYTOPLANKTON POPULATIONS ON GEORGES BANK[1]

By

GORDON A. RILEY

Woods Hole Oceanographic Institution

and

Bingham Oceanographic Laboratory

A complex field such as oceanography tends to be subject to two opposite approaches. The first is the descriptive, in which several quantities are measured simultaneously and their inter-relationships derived by some sort of statistical method. The other approach is the synthetic one, in which a few reasonable although perhaps over-simplified assumptions are laid down, these serving as a basis for mathematical derivation of relationships.

Each approach has obvious virtues and faults. Neither is very profitable by itself; each requires the assistance of the other. Statistical analyses check the accuracy of the assumptioms of the theorists, and the latter lend meaning to the empirical method. Unfortunately, however, in many cases there is no chance for mutual profit because the two approaches have no common ground. Until such contact has been established no branch of oceanography can quite be said to have come of age. In this respect physical oceanography, one of the youngest branches in actual years, is more mature than the much older study of marine biology. This is perhaps partly due to the complexities of the material. More important, however, is the fact that physical oceanography has aroused the interest of a number of men of considerable mathematical ability, while on the other hand marine biologists have been largely unaware of the growing field of bio-mathematics, or at least they have felt that the synthetic approach will be unprofitable until it is more firmly backed by experimental data.

However valid the latter objection may be, the present paper will attempt, in the limited field of plankton biology, to establish continuity between some purely descriptive studies that have been made and mathematical concepts based on what seem to be logical assumptions about plankton physiology. The need for such an attempt has

[1] Contribution No. 353 from the Woods Hole Oceanographic Institution.

become apparent during the course of several plankton surveys in which the data were analyzed statistically with the idea of correlating plankton populations and their rate of growth with various environmental factors such as solar radiation, temperature, dissolved nutrient salts, *etc.* In each survey a reasonably high degree of correlation was found, but the empirical nature of the relationships was often confusing. For example, temperature affects plankton in several different ways, and the relative importance of these effects varies from time to time and from place to place. The statistical relationship of temperature and plankton represents an average of these different effects. Therefore, it may happen in examining sets of data for particular areas and times that the temperature constant varies widely from set to set, and study of the values of their constants does not lead easily to a universally applicable theory.

Furthermore, there is no good reason for assuming that the variations of plankton with environment are always linear. To treat them as such may introduce an error. To evolve nonlinear relationships on a purely empirical basis is possible, but this generally requires a larger set of observations than is readily available.

These limitations of the statistical method will become apparent in the pages that follow. The only way to avoid them is by the opposite approach—that of developing the mathematical relationships on theoretical grounds and then testing them statistically by applying them to observed cases of growth in the natural environment. At present this can be done only tentatively, with over-simplification of theory and without the preciseness of mathematical treatment that might be desired. It is not expected that any marine biologist, including the writer, would fully believe all the arbitrary assumptions that will be introduced. However, the purpose of the paper is not to arrive at exact results but rather to describe promising techniques that warrant further study and development.

ACKNOWLEDGMENTS

My best thanks are due Dean F. Bumpus, who kindly provided me with the necessary zooplankton data, and Henry Stommel, who gave me valuable advice on some of the mathematical treatment.

STATISTICAL SECTION

Phytoplankton studies in the Georges Bank area of the western North Atlantic during the period from 1939 to 1941 have been described in a series of publications (Riley, 1941, 1942, 1943; Riley and Bumpus, 1946). In the first of these papers it was noted that part of

the variations that occurred in the distribution of phytoplankton from one part of the bank to another and from one month to the next could be correlated with such factors as the depth of water, temperature and dissolved phosphate and nitrate. Since that time the study of the zooplankton collections has been completed and examination of the data has shown that grazing by zooplankton is important in controlling the size of the phytoplankton population. With the inclusion of the zooplankton material, it is now possible to develop a relatively complete statistical treatment of the ecological relationships of the Georges Bank plankton.

Observations. The original observations made during the 1939–1940 cruises were listed in the papers cited above. This material is briefly summarized in Table I in the form of means and standard deviations for each cruise. Correlations of phytoplankton with its various environmental factors have also been published. These have been

TABLE I. Means and Standard Deviations of Georges Bank Plankton and Environmental Factors

		Sept.	*Jan.*	*Mar.*	*Apr.*	*May*	*June*
Mean	*Depth of water in meters*	247	209	135	209	82	206
	Mean temperature, upper 30 m.	15.24	4.61	2.60	3.81	5.14	9.66
	Mg-atoms phosphate P per m², upper 30 m.	14.4	33.7	34.7	21.9	16.6	19.2
	Mg-atoms nitrate N per m², upper 30 m.	153	209	172	129	285	155
	Number of animals, thousands per m²	135	14	24	32	106	103
	Plant pigments, thousands of Harvey units per m²	560	118	828	2303	871	478
σ	*Depth*	540	371	163	530	357	458
	Temperature	2.14	0.71	0.33	0.37	0.39	2.58
	P	7.2	11.1	8.1	8.9	3.5	8.7
	N	108	209	68	129	79	155
	Zooplankton	126	13	18	38	77	85
	Plant pigments	195	67	781	827	522	233

used to develop multiple correlation equations by which the variations in horizontal distribution of plant pigments during each cruise are calculated according to the variations in environmental factors. Comparison of calculated values with the actual determinations for plant pigments shows an average error on the different cruises of 20–40%. In other words 60–80% of the variations in phytoplankton on Georges Bank can be accounted for on the basis of variations in depth, temperature, phosphate, nitrate and zooplankton. The multiple correlation equations for each cruise are as follows:

Sept.: $PP = -.011D - 23.8t + 5.20P + .371N - .26Z + 829$

Jan.: $PP = .191D - 61.2t + 7.96P + .956N + .47Z - 115$

Mar.: $PP = -D - 770t - 23.18P - 6.98N - .62Z + 4989$

Apr.: $PP = .469D - 331t - 61.4P + .197N - 5.31Z + 4954$

May: $PP = .007D + 236t + 15.1P - 2.316N - 3.50Z + 437$

June $PP = -.066D - 48.1t - 15.5P + .070N - .55Z + 1300$

PP is thousands of Harvey units of plant pigments per m^2, D is depth of water, t is temperature, P is mg-atoms of phosphate P per m^2 in the upper 30 meters, N is mg-atoms of nitrate N, and Z is thousands of animals per m^2.

Discussion of the effect of environmental factors on the horizontal distribution of phytoplankton. The equations show, within the limits of error stated above, the amount of variation in the phytoplankton crop that is obtained by varying any one or all of the environmental factors. For example, at a particular station of the September cruise, if all the factors were found to have exactly the mean values as stated in Table I, then the plant pigments would be expected to have the mean value for September. If phosphate were increased one milligram-atom, it would increase the calculated value for plant pigments by the amount of the phosphate constant, or 5.2 thousands of units. If the phosphate varied a "normal" amount, as indicated by the limits of its standard deviation, the plant pigments would be changed ± 6.5%. Use of the standard deviation in this way is a convenient method of rating the importance of a given factor, and in Table II it is applied to all the variables in the equations. Although the standard deviation is a positive or negative variation around the mean, it serves a useful purpose to give the values in the table the same sign as the constant in the equation. The figures then represent the change in plant pigments produced by raising each factor from its mean to the upper limit of its standard deviation.

Table II shows that although one particular factor may be of outstanding significance, such as nitrate during the March cruise, phos-

TABLE II. Percentage Change in the Phytoplankton Crop Produced by Increasing the Value of Each Environmental Factor from Its Mean to the Limit of Its Standard Deviation

	Sept.	*Jan.*	*Mar.*	*Apr.*	*May*	*June*
Depth	−1	60	−20	11	0	− 1
Temperature	−9	−37	−31	− 5	10	−26
P	7	74	−23	−24	6	−28
N	7	41	−57	1	−21	1
Zooplankton	−6	5	− 1	− 9	−31	−10

phate in April, and zooplankton in May, there is no indication of complete control of the phytoplankton crop by a particular factor. It appears to be a highly complex relationship in which one factor after another gains momentary dominance. This table also shows that each variable has a vastly different significance at different times of the year, which is in accord with our present knowledge of phytoplankton ecology.

It has been shown (Riley, 1942) that the depth of water plays a significant role in the inception of the spring diatom flowering, and it is reasonable to find a strong negative relationship in March. This effect disappears later in the season when radiation becomes strong enough so that vertical turbulence is no longer able to prevent growth by dissipating the surface crop.

Temperature is generally supposed to have a negative effect on phytoplankton because increased respiration uses up part of the store of energy that would otherwise be used in the production of new plant material. The predominantly negative relationship shown in Table II is therefore expected. The positive relation in May is anomalous and not readily explainable.

The nutrient-phytoplankton relationship is one in which cause and effect are not clearly separable; although a large quantity of available nutrients is likely to stimulate growth, the growth-utilization process will reduce the quantity of nutrients so that the relationship becomes negative. The diversified results in Table II come from the complexities of this inter-relation. Probably the relationships are of three main types. First, in January, when the quantity of available nutrients was large and growth was slight because of low light intensity, the observed positive relationship is indicative of a slight stimulating effect by nutrients, which to a slight degree counteracted the inhibiting effect of insufficient light. Second, in spring, when radiation increased and growth became more abundant, negative relationships of the growth-utilization type were established. However, they did not become progressively stronger with the advance of the season, leading to complete exhaustion of nutrients; whether or not the observed partial exhaustion had an inhibiting effect on growth cannot be determined from these data. Third, a situation was established which was particularly apparent in September but which probably began early in the summer; in this situation the total quantity of plant pigments was fairly uniform all over the bank, but with certain localized areas of slightly higher crops accompanied by larger quantities of nutrients. These were sufficiently important to provide a direct relationship of a moderately low order between plankton and nutrients. They included some shallow water stations as well as four in deeper

water (50 to 100 m.) on the northern and western edges of Georges Bank. In all cases the vertical distribution of temperature, as well as nutrients, was more nearly uniform than at near-by stations that had smaller crops. It is concluded, therefore, that the observed relationship was due to localized turbulence and upwelling of the nutrient-rich lower waters. Probably such conditions were of transient nature, for it seems likely that a degree of regeneration strong enough to maintain a positive nutrient-phytoplankton relationship for any length of time would lead to a much larger growth than was observed.

The phytoplankton-zooplankton relationship has been discussed in some detail in a previous paper (Riley, 1946) and need be only briefly summarized here. It was concluded that the predominantly negative relationship was due to grazing. The quantities of animals and plants were such as to indicate that the observed relationship could have been established in a very short time, possibly in a day or in a few days. A theory was postulated that tidal currents and turbulent motion of the Georges Bank waters tended continually to destroy the horizontal gradients in phytoplankton, but that the zooplankton, because of their habit of vertical migration, would be absent part of the time from the surface waters where mixing processes are strongest, and hence they would not be so readily dispersed. Therefore, they would tend constantly to reestablish the phytoplankton gradients by their grazing activity.

Effect of Environmental Factors on the Seasonal Cycle of Phytoplankton. It is apparent from the preceding discussion that the relationship of a particular environmental factor with the horizontal distribution of phytoplankton may differ from one month to another both in quantity and in kind. Nevertheless, there are seasonal trends in these factors which are related with plankton variations, as can be observed by inspection of the data in Table I. Thus the seasonal cycle of phytoplankton can be correlated with its environment with a fair degree of accuracy, even though such treatment makes no allowance for special effects that are operative only at particular times during the year.

A multiple correlation equation was developed from the cruise averages in Table I. It is

$$PP = -153t - 120P - 7.3N - 9.1Z + 6713.$$

The symbols are the same as in previous equations. The relation between the observed cruise averages and the values determined from the equation is shown in Fig. 14. The average error between observed and calculated values is 20%, which is slightly less than that obtained in the treatment of individual cruises. Probably the errors caused by

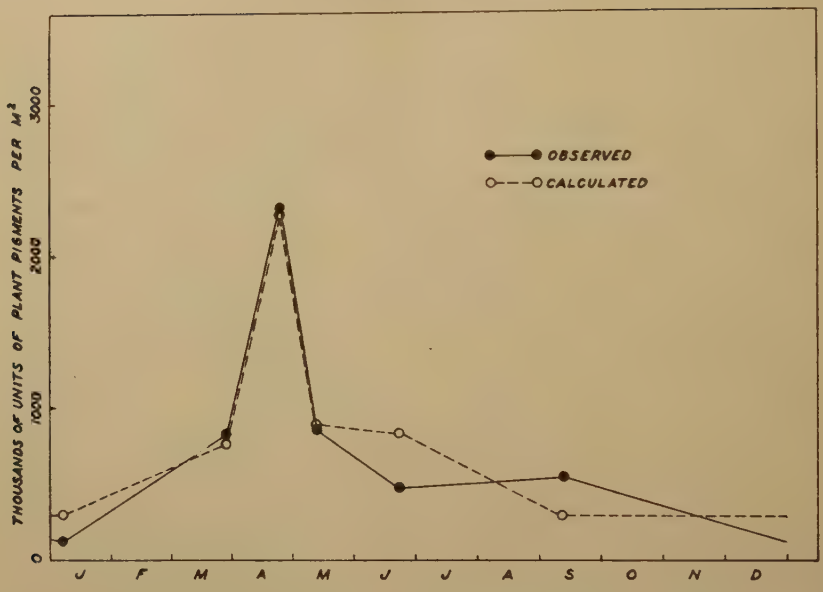

Figure 14. Comparison of the observed phytoplankton population with the calculated population as determined by a multiple correlation analysis of the relationship between phytoplankton and environmental factors.

ignoring certain special seasonal effects are more than counterbalanced by the reduction in analytical errors when averages are used for the calculation.

THEORETICAL SECTION

The rate of change of the phytoplankton population is determined by the difference in reaction rates between the process of accumulation of energy by the population and the processes of energy dissipation. It will be assumed that all the important reaction rates are included in the equation

$$\frac{dP}{dt} = P\,(P_h - R - G)\,, \tag{1}$$

in which the rate of change of the population P in respect to time is determined by the photosynthetic rate per unit of population (P_h), the rate of phytoplankton respiration (R), and the rate of grazing by zooplankton (G). Each of these rates is subject to environmental influences and therefore is continually changing with the seasons. In order to arrive at a practical solution of the equation it is necessary to examine each of its component parts in the light of present day plankton physiology.

A second major assumption will be that seasonal variations in environmental factors used in the analysis can be expressed by smooth curves drawn through the observed cruise averages. Since the latter are relatively incomplete, as far as the whole yearly cycle is concerned, there must be a certain amount of unavoidable error in the calculations.

Photosynthesis. Numerous investigators have reported that the photosynthetic rate in actively growing diatom cultures is proportional to light intensity within wide limits. The lower limit has not been determined accurately due to the insensitivity of the methods of measurement, but values of the right order of magnitude have been detected at depths where the light intensity was about 0.1–1.0% of the surface intensity in summer (Clarke, 1936). The upper limit of the proportionality is variable, depending on the species and the length of exposure; the optimum intensity for photosynthetic activity in particular situations has been reported to range from 1.8 g. cal. per cm^2 per hour (Jenkin, 1937) to 60 g. cal. (Curtis and Juday, 1937).

During the six cruises to Georges Bank between September 1939 and June 1940 two bottles of surface water were taken at each station and suspended in a tub of water on deck, one of them being covered with a bag of several thicknesses of dark cloth. After twenty-four hours' exposure the oxygen in the two bottles was measured and the difference in their oxygen content was used as a rough estimate of the photosynthetic activity of the surface plankton. The inset in Fig. 15 shows the average photosynthetic rate[2] obtained on each cruise plotted against the average incident solar radiation in the area at that time of year. Radiation values are obtained from data published by Kimball (1928) and reproduced in Sverdrup, Johnson and Fleming (1942: 103). The plotted points for the January, March, April and May cruises approximate a linear relationship in which the photosynthetic rate equals 2.5 times the incident radiation in g. cal. per cm^2 per minute. The June and September rates are lower, but it will be shown later that this can be explained as a result of nutrient depletion.

With these facts at hand the mean photosynthetic rate of the population will be estimated according to the following assumptions:

1. When nutrient depletion does not limit photosynthesis,

$$P_h = pI \qquad (2)$$

[2] The photosynthetic rate is expressed as grams of carbon produced per day per gram of carbon in the surface phytoplankton crop, using the formula photosynthetic rate = .375 × oxygen production in g/m^3/day ÷ 17 × 10^{-6} Harvey units of plant pigments/m^3. The conversion factor is based on analyses described in a previous paper on the plankton of Georges Bank (Riley, 1941).

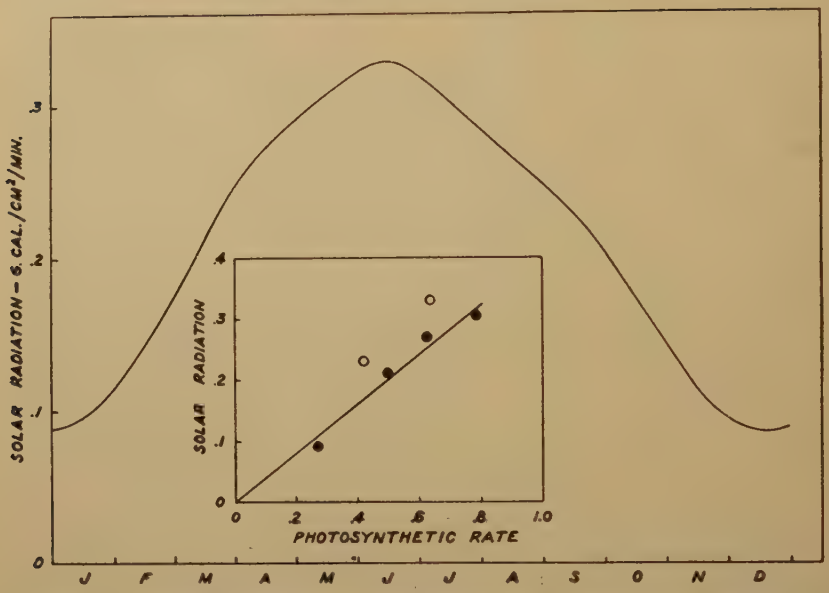

Figure 15. Seasonal variations in average incident solar radiation in the Georges Bank area. Inset shows average observed surface photosynthetic rate plotted against incident radiation. Dots are averages for January, March, April and May; circles are June and September.

in which P_h is the photosynthetic rate, I is radiation in g. cal./cm²/minute at the depth of the photosynthesizing plankton, and p, the photosynthetic constant, is 2.5.

2. The intensity at the surface, I_o, may be determined for any time in the year from the curve in Fig. 15, which is based on Kimball's data, cited above.

3. The intensity at any other depth z is determined from the formula

$$I_z = I_o e^{-kz}$$

and therefore

$$P_{hz} = pI_o e^{-kz}. \qquad (3)$$

In these formulas the extinction coefficient k is defined as 1.7 divided by the depth of the Secchi disc reading, a rough conversion factor suggested by Poole and Atkins (1929). Secchi disc determinations for the Georges Bank area are shown in Fig. 16.

4. According to equation (3) the photosynthetic rate approaches zero as the depth approaches infinity. But the depth at which a measurable and significant amount of photosynthesis occurs is limited, and so is the depth at which viable phytoplankton can be found.

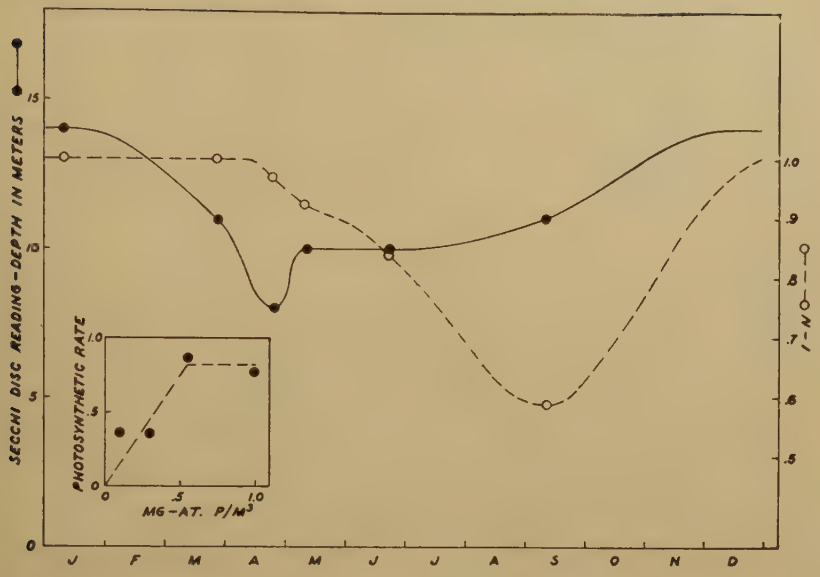

Figure 16. Solid curve is transparency as determined by Secchi disc readings. Dotted line is the estimated reduction in photosynthetic rate caused by nutrient depletion. Inset shows averages of photosynthetic rate plotted against phosphate concentration during June and September.

Therefore, it is convenient to set an arbitrary limit to the depth of the euphotic zone. This depth will be called z_1 and will be defined as the depth at which the light intensity has a value of 0.0015 g. cal./cm²/minute. This approximates the intensity at the maximum depth of photosynthesis as reported by Clarke (1936). Calculated values for z_1 are shown in Fig. 17.

5. To find the mean photosynthetic rate in the euphotic zone, equation (3) is integrated from the surface to z_1, and divided by z_1:

$$\overline{P_h} = \frac{pI_o \int_o^{z_1} e^{-kz}\,dz}{z_1} = \frac{\dfrac{pI_o}{-k}\, e^{-kz}\Big|_o^z}{z_1}$$

$$\underset{o \to z_1}{\overline{P_h}} = \frac{pI_o}{kz_1}(1 - e^{-kz_1}). \qquad (2)$$

6. It was postulated that the proportionality between photosynthesis and radiation holds only when nutrients are abundant. The fact noted previously that the ratio between the photosynthetic rate and light intensity was reduced in June and September led to an in-

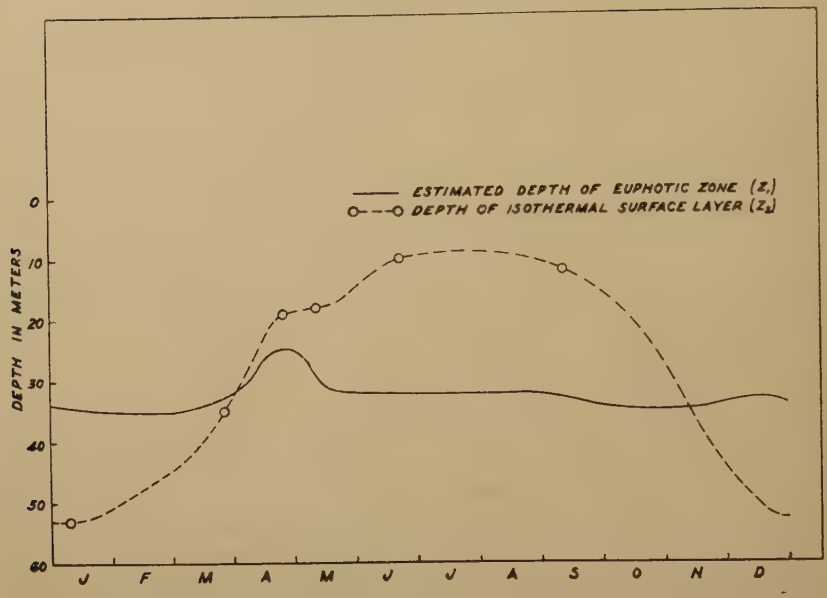

Figure 17. Estimated depth of the layer in which a measurable amount of photosynthesis occurs (z_1), and the depth of the virtually isothermal surface layer (z_2).

vestigation of nutrients as a possible cause. Large individual variations were found, and the correlation between photosynthetic rate and phosphate concentration was poor; nevertheless, when the rates were averaged for different ranges of phosphate concentration, there was a pronounced reduction in the average rate when the phosphate fell below about 0.5 to 0.6 mg-atom of P per m^3 (Fig. 16, inset). Ketchum (1939) reported a decrease in the growth rate of experimental cultures of *Nitschia closterium* when the phosphate concentration was less than 50 gamma of PO_4 per liter (0.55 mg-atom per m^3). Therefore it seems reasonable to assume that the mean photosynthetic rate as determined in equation (4) should be multiplied by a factor $(1 - N)$, in which N is the reduction in rate due to nutrient depletion. According to the facts above,

$$N = \frac{0.55 - \textit{mg-at. } P/m^3}{0.55} \qquad \text{when } P \leqq 0.55.$$

Mean values for $(1 - N)$ are shown in Fig. 16.

7. Several investigators have pointed out the importance of vertical turbulence in reducing phytoplankton crops by carrying the breeding stock below the euphotic zone. That this is an important phenomenon on Georges Bank has been demonstrated (Riley, 1942). If turbulence

is such that each phytoplankton cell spends only a certain proportion of its time in the euphotic zone, then the mean photosynthetic rate of the population as a whole will be reduced. Therefore equation (4) should be multiplied by still another factor $(1 - V)$, in which V is the reduction in rate produced by vertical water movements. It is impossible to define V in any simple way that will be entirely satisfactory, but as an approximation,

$$(1 - V) = \frac{z_1}{z_2} \text{ when } z_1 \leqq z_2,$$

in which z_1 is the depth of the euphotic zone as previously defined and z_2 the depth of the mixed layer, which is arbitrarily defined as the maximum depth at which the density is no more than 0.02 of a σ_t unit greater than the surface value. Fig. 17 shows the estimated values for z_1 and z_2 for Georges Bank.

The final equation for the mean photosynthetic rate is now

$$P_h = \frac{pI_o}{kz_1}(1 - e^{-kz_1})(1 - N)(1 - V). \qquad (5)$$

The application of the equation to the Georges Bank data is shown in Fig. 18. The upper curve shows the primary calculation of the photo-

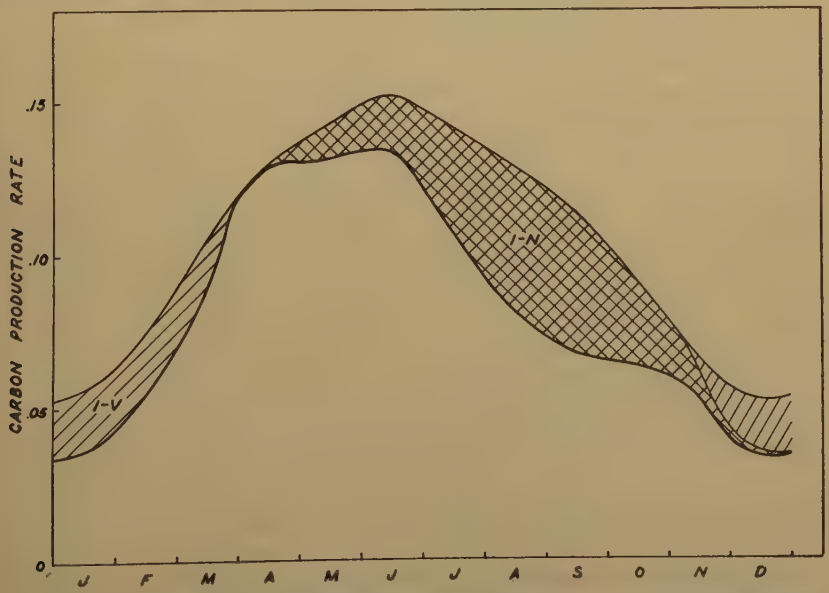

Figure 18. Estimated mean photosynthetic rate. Upper curve is the maximum possible rate as determined by incident radiation and transparency. Lower curve is the estimate obtained by introducing correction factors for the effects of vertical turbulence and nutrient depletion.

synthetic rate based on light intensity. The reduction obtained by introducing $(1 - N)$ and $(1 - V)$ is indicated by hatched areas. The heavy lower curve is the final estimate of the mean photosynthetic rate.

Phytoplankton respiration. The few available measurements of the respiration of pure diatom cultures have not yielded precise results. Observed rates have varied from one species to another as well as during different stages of growth of the same culture. The recorded values differ by a factor of 10 to 20, and there are not enough of them to draw a good average.

No direct measurements have been made of the respiration of a natural phytoplankton population, since the measured oxygen consumption also includes zooplankton and bacterial respiration. Statistical estimates have been made by the writer on the basis of the observed correlation between phytoplankton and total oxygen consumption. The best of these, judging by quantity and homogeneity of data, was obtained in Long Island Sound (Riley, 1941a). It was estimated that in winter (average temperature 2.05° C.) the respiration rate was 0.024 ± 0.012 mg. of carbon consumed per day per mg. of phytoplankton carbon. Calculations based on summer observations suggested that the respiration increased with higher temperatures (0.110 ± 0.007 at 17.87° C.), the rate being approximately doubled by a 10° increase in temperature.

On the basis of these rather scanty data it will be assumed that:

1. The temperature effect can be stated as

$$R_T = R_o e^{rT} \tag{6}$$

in which R_T is the respiratory rate at any temperature T, R_o is the rate at 0° C. and r is a constant expressing the rate of change of the respiratory rate with temperature. The value of r is 0.069 when the rate is doubled by a 10° increase in temperature. The seasonal cycle of Georges Bank surface temperatures used in computing respiratory rates is shown in Fig. 19.

2. The value chosen for R_o will be 0.0175. This is the mean of the two estimates derived from the Long Island Sound data mentioned above, in which the calculated values of R_o for winter and for summer are respectively 0.020 and 0.015.

Grazing. The greater part of the zooplankton population consists of filter-feeding organisms which tend to strain a relatively constant volume of water in a given time irrespective of the quantity of food material in it. Therefore a fixed proportion of the phytoplankton population will be consumed in successive units of time. This is stated as

$$G = gZ\,, \tag{7}$$

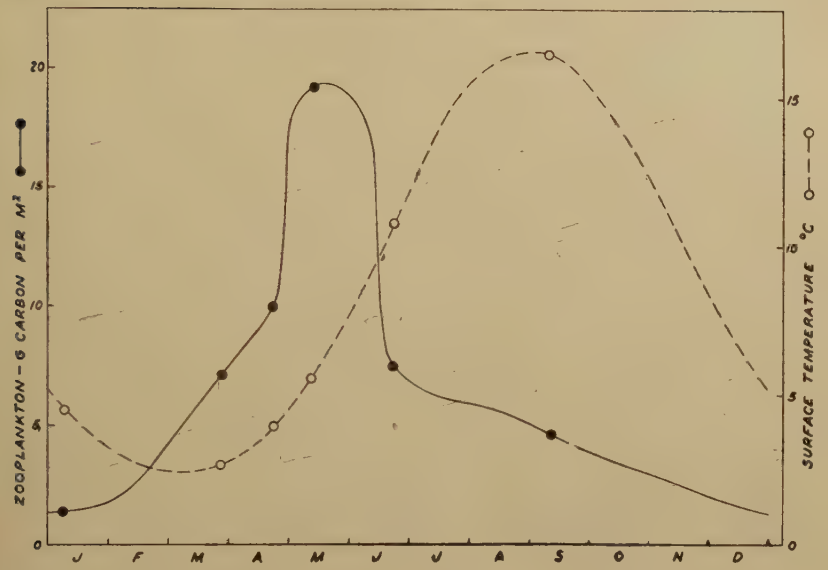

Figure 19. Solid line is the seasonal cycle of zooplankton. Measurements of zooplankton volume by the displacement method are treated by a conversion factor (wt. in g. = 12.5% × vol. in cc.) to derive a rough estimate of the carbon content. Dotted line is the mean surface temperature.

in which G is the rate of grazing, g is the rate of reduction of phytoplankton by a unit quantity of animals and Z is the quantity of zooplankton in grams of carbon per m².

There is some question as to whether g is nearly constant over long periods of time or undergoes a marked seasonal change. On the one hand there are the experiments of Marshall, Nicholls and Orr (1935) which showed that the respiratory rate of *Calanus finmarchicus* increases with increasing temperature, implying a greater food requirement at higher temperatures and possibly an increased filtering rate. On the other hand, feeding experiments by Fuller (1937) showed variations of a more complex nature. The grazing rate of *Calanus finmarchicus* was greater at 8° C. than at 3° or 13° C., and animals captured in the late summer, when the natural breeding stock was declining, had lower feeding rates than those studied earlier in the summer. Thus a factor that can be called "depressed physiological state" for want of a more precise term appears to counterbalance the expected effect of high temperature late in the summer. It is clear that the whole process of zooplankton feeding requires much more thorough study. However, lacking the necessary information to de-

scribe the process accurately, it is believed that it can best be approximated by the simple form of equation (7).

The value of g must be of an order of magnitude which will at least satisfy the minimum respiratory requirements of the zooplankton population at times when the latter is stable. According to Marshall, Nicholls and Orr (1935), the daily food requirement of *Calanus* in winter (5° C.) lies between 1.3 and 3.6% of the carbon content of the animals. This estimate applied to the January plankton on Georges Bank yields a grazing constant of 0.0091 to 0.0252. In summer (15° C.), these authors suggest a food requirement of 1.7–7.6%, for which the corresponding values of g are 0.0084 to 0.0374 in September on Georges Bank. The latter estimates are perhaps too high, since the zooplankton was decreasing at a rate of 0.5% per day and therefore probably was not getting enough food to satisfy the minimum respiratory requirements. If it is assumed that the food intake equaled the food requirement minus the rate of population decrease, then the food intake was 1.2–7.1% of the animals' carbon content per day, and the corresponding values for g are 0.0059 and 0.0350.

Within these wide limits it is difficult to choose a correct value for the grazing constant, and again the need for more experimental work is apparent. On a purely empirical basis, a good fit for the data is obtained by using the average of the minimum values of g for the September and January cruises, namely 0.0075. This factor, multiplied by the quantity of zooplankton, shown in Fig. 19, estimates the Georges Bank grazing rate.

Conclusions. The original equation

$$\frac{dP}{dt} = P\,(P_h - R - G)$$

can now be expanded by substituting the right hand terms of equations (5), (6) and (7):

$$\frac{dP}{dt} = P\left[\frac{pI_\circ}{kz_1}\,(1 - e^{-kz_1})\,(1 - N)\,(1 - V) - R_\circ e^{rT} - gZ\right]. \quad (8)$$

The rate of change of the population is dependent on six ecological variables: the incident solar radiation, transparency of the water, the quantity of phosphate, the depth of the mixed layer, the surface temperature and the quantity of zooplankton. The results of the application of equation (8) to the Georges Bank data are shown graphically in Fig. 20. The curve at the top is the photosynthetic rate previously illustrated (Fig. 18). The second curve is the photosynthetic rate minus the respiratory rate of the phytoplankton, or in other words the

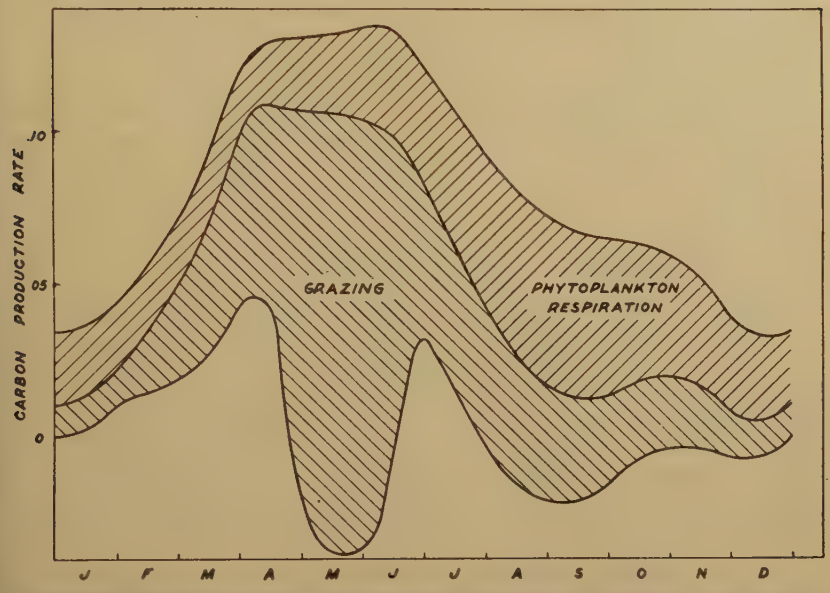

Figure 20. Estimated rates of production and consumption of carbon. Curve at top is the photosynthetic rate. By subtracting the respiratory rate the second curve is obtained, which is the phytoplankton production rate. From this is subtracted the zooplankton grazing rate, yielding the curve at the bottom, which is the estimated rate of change of the phytoplankton.

phytoplankton production rate. By subtracting the grazing rate from the production rate, the rate of change of the population is obtained. This is the bottom curve of Fig. 20. Numerical values used in drawing these curves are shown in the appendix.

Equation (8) cannot be integrated readily, but an approximation is obtained by integrating over successive short intervals of time and assuming for each variable a constant, average value during that time. Thus the change in population in the time interval 0 to t is determined by

$$lnP_t - lnP_0 = \overline{P_h} - \overline{R} - \overline{G}\,.$$

Therefore, by a series of integrations the quantity $lnP_t - lnP_0$ can be approximated for the whole seasonal cycle. This quantity indicates the relative size of the population from one part of the cycle to another. To convert to absolute terms requires evaluation of the integration constant P_0 (the size of the population at the minimum point in the cycle), which is readily obtained if the quantity of plankton (P_t) is measured at one or more times during the year. In the present case, in which six cruise averages are available, P_0 was statistically deter-

mined so as to give the best fit for the data. The results are shown in Fig. 21, in which the theoretical population cycle is shown by a smooth curve, and the observed cruise averages are indicated by dots. The average error is 27%.

It is now apparent that a few simple and commonly measured environmental factors can be used with a fair degree of accuracy to evaluate the quantitative aspects of the seasonal cycle of phytoplank-

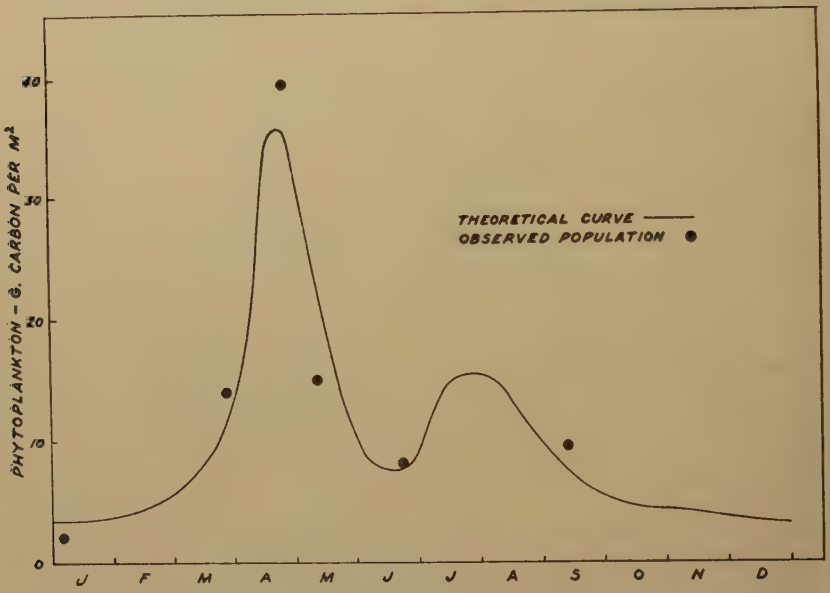

Figure 21. Curve shows the calculated seasonal cycle of phytoplankton, determined by approximate integration of the equation for the rate of change of the population. For comparison the observed quantities of phytoplankton are shown as dots.

ton. Furthermore, this can be done in two different ways: first by statistical comparison of the simultaneous variations of phytoplankton and environmental characteristics in a particular locality; second, by theoretical evaluation of the way in which changes in the environment might affect growth as evidenced by the results of various physiological experiments. Each of these methods has something to contribute to plankton biology. The statistical method is useful in determining whether a particular factor is significant; the theoretical method carries on from there, discriminating between cause and effect and helping to establish certain quantitative relationships that are not likely to be derived empirically.

While these methods are obviously crude at the present time and need to be developed further, both by examination of other areas and by better experimental evaluation of constants, it does not seem too much to hope that they will eventually solve some of the problems of seasonal and regional variations that puzzle marine biologists today.

SUMMARY

1. Variations in the phytoplankton population of the Georges Bank area are correlated with various environmental factors. Equations are developed statistically by which the size of the population can be calculated on the basis of such factors as temperature, depth of water, and the quantities of nitrate, phosphate and zooplankton. Calculated horizontal variations in the plankton crop at various times in the year differ from observed values by about 20–40%. Calculations of the seasonal variation of the average crop in the area are accurate within about 20%.

2. The seasonal cycle of phytoplankton is also evaluated from a more theoretical standpoint. It is postulated that the rate of change of the phytoplankton population is equal to the photosynthetic rate minus the phytoplankton respiratory rate minus the grazing rate of the zooplankton. Factors affecting these rates are discussed, and the ones that are considered particularly important are solar radiation, temperature, transparency of the water, the depth of the isothermal surface layer, phosphate, and zooplankton. The observed variations of these factors are combined with appropriate constants derived from experimental data to develop an equation that expresses the seasonal rate of change of the phytoplankton population. Approximate integration of the equation yields a population curve of the same order of accuracy as the statistical estimate.

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APPENDIX

NUMERICAL VALUE OF QUANTITIES USED IN THE CALCULATION OF THE SEASONAL RATE OF CHANGE OF THE GEORGES BANK PHYTOPLANKTON POPULATION AS DEVELOPED IN THE THEORETICAL SECTION OF THIS PAPER

Date	I_o	k	z_1	$1-N$	z_2	$1-V$	P_h	T	R_T	Z	G	dP/dt	$lnP_t - lnP_o$	lnP_t	P_t
1/1	.088	.121	34	1.00	53	.64	.034	5.2	.024	1.3	.010	.000	.000	1.217	3.4
1/15	.094	.121	34	1.00	53	.64	.036	4.1	.023	1.4	.011	.002	.030	1.247	3.5
2/1	.112	.124	35	1.00	51	.69	.044	3.2	.021	1.7	.013	.010	.180	1.397	4.0
2/15	.138	.128	35	1.00	48	.73	.055	2.7	.021	2.6	.020	.014	.390	1.607	5.0
3/1	.174	.136	35	1.00	45	.78	.071	2.4	.021	4.2	.031	.019	.675	1.897	6.7
3/15	.212	.145	34	1.00	40	.85	.091	2.5	.021	5.8	.043	.027	1.080	2.297	10.0
4/1	.247	.159	32	1.00	32	1.00	.120	2.7	.021	7.5	.056	.043	1.725	2.942	19.1
4/15	.272	.200	26	1.00	23	1.00	.130	3.4	.021	8.9	.067	.042	2.355	3.572	35.5
5/1	.290	.205	25	.95	19	1.00	.131	4.5	.024	17.2	.129	−.022	2.025	3.242	25.7
5/15	.306	.170	31	.92	18	1.00	.132	5.9	.026	19.3	.145	−.039	1.440	2.657	14.2
6/1	.321	.170	32	.90	15	1.00	.134	7.6	.030	18.8	.141	−.037	.885	2.102	8.2
6/15	.329	.170	32	.88	11	1.00	.134	9.7	.035	14.0	.105	−.006	.795	2.012	7.5
7/1	.319	.170	32	.82	10	1.00	.122	11.8	.038	6.9	.052	.032	1.275	2.492	12.1
7/15	.302	.170	31	.76	9	1.00	.108	13.9	.045	6.2	.047	.016	1.515	2.732	15.4
8/1	.284	.165	32	.69	9	1.00	.093	15.5	.051	6.0	.045	−.003	1.470	2.687	14.8
8/15	.267	.162	32	.63	10	1.00	.081	16.3	.054	5.7	.043	−.016	1.230	2.447	11.5
9/1	.250	.159	32	.60	11	1.00	.073	16.6	.056	5.1	.038	−.021	.915	2.132	8.4
9/15	.230	.154	33	.59	13	1.00	.067	16.4	.054	4.5	.034	−.021	.600	1.817	6.1
10/1	204	.145	34	.63	16	1.00	.065	15.5	.051	3.9	.029	−.015	.375	1.592	4.9
10/15	.174	.138	34	.69	20	1.00	.063	14.2	.045	3.3	.025	−.007	.270	1.487	4.4
11/1	.144	.131	35	.77	27	1.00	.060	12.4	.040	3.2	.024	−.004	.210	1.427	4.2
11/15	.115	.126	35	.85	37	.95	.053	10.5	.037	2.6	.020	−.004	.150	1.367	3.9
12/1	.094	.121	34	.92	45	.76	.039	8.5	.031	2.0	.015	−.007	.045	1.262	3.5
12/15	.086	.121	33	.97	50	.66	.033	6.7	.028	1.6	.012	−.007	−.060	1.157	3.2

I_o = incident solar radiation in g. cal./cm² 1 /cm²/minute

k = extinction coefficient = 1.7/Secchi disc reading in meters

z_1 = depth of euphotic zone in meters, defined as depth where the light intensity is .0015 g. cal.

$1 - N$ = correction factor for nutrient depletion = mg-at. phosphate P/0.55 when $P \leqq 0.55$.

z_2 = depth of mixed layer = maximum depth at which $\sigma_{tz} - \sigma_{t_o} \leqq 0.02$.

$1 - V$ = correction factor for vertical turbulence = z_1/z_2 when $z_1 \leqq z_2$.

P_h = estimated mean photosynthetic rate according to equation (5) in text.

T = mean surface temperature.

R_T = estimated phytoplankton respiration according to equation (6).

Z = g. of zooplankton carbon/m², estimated on the assumption that the weight of carbon in grams = 12.5% of the volume (by displacement) in cubic centimeters.

G = grazing rate = $0.0075Z$

dP/dt = rate of change of the phytoplankton population = $Ph - R - G$.

$lnP_t - lnP_o$ = the summation of 15 × dP/dt (since the rate determinations are at approximately 15-day intervals)

$lnP_t = lnP_t - lnP_o + 1.217$. The latter is a value for P_o determined statistically as the best fit for the observed population data.

P_t = estimated population in g. of phytoplankton carbon/m² (considered equivalent to 17 × Harvey units of plant pigments × 10^{-6}/m²).

A STUDY OF VARIABILITY IN PLANKTON TOW-NET CATCHES OF PACIFIC PILCHARD (*SARDINOPS CAERULEA*) EGGS[1]

By

RALPH P. SILLIMAN

INTRODUCTION

During the pilchard spawning season of 1940 the United States Fish and Wildlife Service, in collaboration with the Scripps Institution of Oceanography, made periodic surveys of part of the pilchard spawning area in an attempt to make quantitative evaluations of egg deposition. In addition to estimating the number of eggs deposited in the entire survey area during the season, it was desired to make estimates of the number of eggs for parts of the area or season in connection with studies of survival, drift of larvae, *etc.* The analysis described below was undertaken for the purpose of gauging the significance and reliability of the estimates of egg concentrations at individual stations, and subsequently for groups of stations. In regard to the variability of the estimates made, there were two questions: (1) the variability in numbers of eggs from 1,000 cubic meter water samples taken at sea as representative of the millions of cubic meters which each station represented in the area of the survey, and (2) the variability of the fractional laboratory samples which were taken to represent the sea samples. To measure variability, both sea and laboratory samples were repeated. Thus, for each station there were four laboratory samples from which the egg concentration could be estimated, *i.e.*, there were two laboratory samples from each of the two sea samples. The statistical study described below was made for the purpose of analyzing the variability or (to use the statistical term) variance of the individual samples into its component parts.

Although the pilchard is known from previous surveys to spawn over an area at least from Oregon to Lower California and out to 300 miles offshore, the major spawning area is confined to a region off southern California which extends from Santa Cruz Island to the Coronados Islands, and 150 miles offshore. It was this smaller area that was covered by the 1940 survey, approximately 40 stations being occupied

[1] Published by permission of the Director, United States Fish and Wildlife Service, Department of the Interior.

on each of six cruises. Stations were arranged on a grid at approximately uniform intervals over the survey area, and the cruises were spaced at uniform intervals during the spawning season (February through June).

Pilchard eggs were collected from the research vessel "E. W. Scripps" by means of pairs of hauls with plankton nets having two square meter mouth areas. The hauls were run successively; the second haul was started as soon as the "cod end" which contained the plankton from the first haul had been removed and replaced with a clean one. Hauls were from 12 to 20 minutes in duration, averaging about 15 minutes. The stray of the towing wire from the vertical was recorded at one minute intervals during each haul to provide a measure of the towing speed; the angle varied from 37° to 55°, with an average of 46°. Current meters were hung in the mouths of the nets during all of the hauls included in the study; the meter readings indicated the length of the water mass which passed through the net. Multiplying these lengths by the area of the mouth gave values of water volumes strained.

Samples of plankton were placed in quart glass fruit jars, with enough 4% formaldehyde solution added to cover the samples. In the laboratory each sample was separated from the preserving liquid, placed in a graduated pitcher, diluted with salt water to a volume of 2,000 cc. and then stirred manually with a spoon, after which 50 cc., or 1/40, of the total stirred plankton suspension was dipped out by means of three dips of a 16 2/3 cc. cream dipper. Pilchard eggs were sorted from the balance of the plankton in the 50 cc. samples and counted, which counts were used in making estimates of egg concentration. At a later date, in order that a study of laboratory sampling variability could be made, the entire procedure was repeated, thus obtaining a second count of pilchard eggs from each sea sample. The "second samples," in all instances covered in this study, were taken by a person other than the one who took the "first samples."[2]

To insure comparability of the data, all material from stations at which the hauling gear did not function properly was discarded. In addition, all stations with a total of less than 15 eggs in either of the pairs of laboratory samples were eliminated, this being done to reduce the variability associated purely with small numbers. After the above eliminations were made the samples from 24 stations, a total of 96 laboratory samples, were at hand for analysis. The numbers of eggs in the samples are given in Table I. Note the great variability, even among those samples which were supposed to represent identical egg

[2] A more detailed description of the gear, method of hauling and laboratory sampling is in preparation by Elbert H. Ahlstrom and will appear in a later publication.

TABLE I—Total Number of Pilchard Eggs Contained in Each Laboratory Sample Used in the Study of Variability

Station Number	*A Hauls*		*B Hauls*	
	1st Sample	*2nd Sample*	*1st Sample*	*2nd Sample*
1102	20	31	32	49
04	13	16	13	21
11	7	17	15	17
30	34	44	110	125
35	9	6	18	14
37	93	63	74	91
38	83	54	70	100
39	37	50	65	66
40	34	37	60	55
1236	44	47	59	65
1315	216	167	177	184
31	44	56	47	50
1404	39	56	48	81
05	57	86	45	70
06	259	299	494	510
09	149	166	124	206
11	30	45	7	10
14	240	250	247	342
18	33	46	22	40
23	20	17	13	12
30	43	45	34	33
34	120	134	96	156
37	16	24	17	31
39	52	63	168	202
Totals	1692	1819	2055	2530
Means	70.50	75.79	85.63	105.42

concentrations. For instance, the counts supposedly representing the concentration at station 1406 varied from 259 to 510 per laboratory sample. The statistical procedure known as the analysis of variance is well adapted to analyzing such variability into its component parts.

ANALYSIS OF VARIANCE[3]

The analysis of variance is designed for use on variates which are normally distributed, or nearly so. Since a frequency distribution of the egg counts given in Table I is J-shaped (Fig. 22) rather than normal, this was remedied by taking logarithms of the individual counts, thus giving a frequency distribution only moderately skewed to the

[3] The aid of C. P. Winsor of Princeton University in the development of the statistical analysis is gratefully acknowledged.

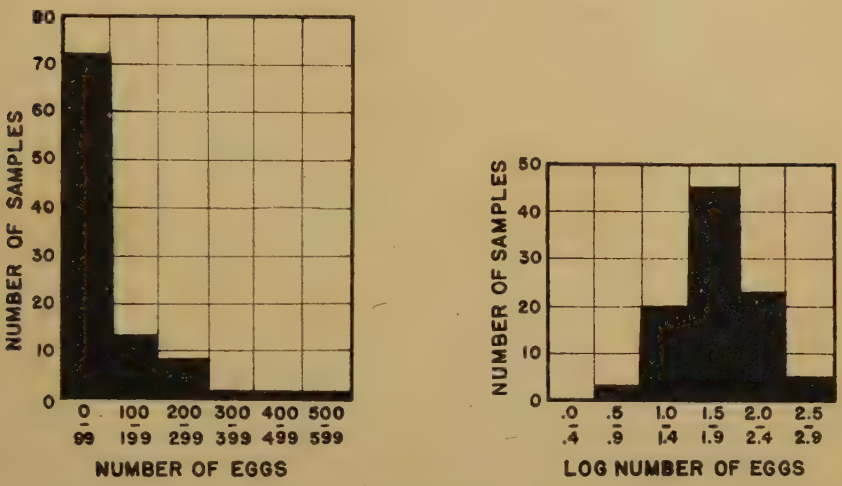

Figure 22. Frequency distribution of pilchard egg counts, in arithmetic and logarithmic forms.

right. Snedecor (1934) considers that the analysis of variance is valid when used with moderately skewed distributions.

The calculations in the following section were carried out in the standard manner (Snedecor, 1934). There was a total of 95 degrees of freedom, which is one less than the total number of samples used in the analysis. The three criteria of classification were station, haul and sample. The arrangement of the degrees of freedom was suggested by C. P. Winsor, and the results are summarized in Table II.

TABLE II—Summary Showing Results of Analysis of Variance

Source of Variation	*Degrees of Freedom*	*Sums of Squares*	*Mean Squares*
Stations	23	15.807	.687
Haul Order	1	.126	.126
Sample Order	1	.157	.157
HO x SO	1	.009	.009
Between hauls, same stations	23	1.231	.054
Between samples, 1st hauls	23	.210	.009
Between samples, 2nd hauls	23	.130	.006

The first feature of the results is the large mean square for "stations," due to actual spatial and temporal differences in egg concentrations. Such differences are not of special interest in the present investigation,

since it is concerned primarily with other types of variability which would lead to error in measuring the spatial and temporal differences.

Next is the relatively large mean square of .126 for "Haul Order," which reflects the fact (shown in Table I) that the B hauls average more eggs than the A hauls. In seeking an explanation for this difference, the entire group of 24 A hauls were compared with the 24 B hauls with regard to both time of hauling and average stray angle, but the distributions of hauling time and average stray angle did not differ significantly from A to B, as indicated by the χ^2 test, nor did their means differ significantly. The only plausible explanation so far advanced is that some eggs from the A haul may have remained in the net and that these were subsequently washed into the cod end during the B haul. Note that the difference between A and B hauls is confined largely to the first nine stations covered by Table I (those occupied during the second cruise of the season). When the hauls for the remaining cruises are compared on a logarithmic basis the difference is very small, indicating an improvement in technique subsequent to the second cruise, probably in respect to the washing of the nets.

The third large mean square, "Sample Order," shows that the second samples average higher counts than the first. Apparently the explanation for this lies in the fact that the second 1/40 samples were taken at a later date and by a different person than the first 1/40 samples; the person who took the first samples used a non-rotary stirring motion, while the person taking the second samples used a rotary stirring motion and dipped the sample from the center of the container, which technique tended to take too large a sample of plankton, since suspended material in a rotating water mass tends to collect at the center of the containing vessel or revolving water mass.

Having considered *consistent* differences between the counts, let us turn to *random* differences, which are more pertinent to the application of this study. The randon variability of the laboratory sampling is measured by the two "Between samples" mean squares in Table II. Although there is a difference between these two it is not significant ($F = 1.60$ as against a value of 2.00 for $P = .05$ in Snedecor's table) and the two variances may be pooled, which gives a sum of squares of .340 for "Between samples," with 46 degrees of freedom. The new mean square is thus .007. In conjunction with the "Between hauls" mean square of .054 (Table II) this may be used to estimate the variance associated with hauls, following the system described by Winsor and Clarke (1940):

Mean square "Between hauls at same station" $= 2\sigma_H^2 + \sigma_S^2 = .054$

Mean square "Between samples" $= \sigma_S^2 = .007$.

Solution of these equations gives $\sigma_H^2 = .024$ as the variance of hauls and $\sigma_S^2 = .007$ as the variance of samples. Therefore $\sigma_H = \sqrt{.024} = .155$, and $\sigma_S = \sqrt{.007} = .084$. The 95% fiducial limits are of interest, and may be calculated from these estimates of σ. For hauls $2 \times .155 = .310$ (2σ limits include 95% of the distribution). Since these values are logarithmic, the antilogs are used to convert to ratios. The antilog of .310 is 2.04, giving fiducial limits of 49% ($100 \times 1/2.04$) to 204% (100×2.04). Thus the egg number from one haul may not be considered significantly different from the egg number at another unless it is less than one-half, or more than double, that of the other. Similarly, the 95% fiducial limits for samples are 68% to 147%, and may be interpreted in a like manner.

To obtain an estimate of total random variability for a single count from a single haul, the haul variance is added to the sample variance, giving $\sigma_C^2 = \sigma_H^2 + \sigma_S^2 = .024 + .007 = .031$. Then $\sigma_C = \sqrt{.031} = .176$, and the 95% fiducial limits calculated as above are 44% to 225%. Again the "half or double" rule approximately applies.

For the 1940 survey the estimates of egg concentration were based on the mean of the four samples from the two hauls at each station. Here $\sigma_C^2 = \frac{1}{2}\sigma_H^2 + \frac{1}{4}\sigma_S^2 = .012 + .002 = .014$. The 95% fiducial limits become 58% to 172%.

RELATION OF SIGNIFICANCE TO NUMBERS COUNTED

Winsor and Walford (1936) concluded, on the basis of an analysis of certain published data on paired hauls, that the accuracy of estimates derived from plankton hauls increases with the number of organisms counted. The central part of their study is based on a regression diagram (Winsor and Walford, fig. 1) showing the relation between sums of catches and estimates of χ^2, the points plotted being averages of groups of values calculated for individual pairs of hauls. For purposes of comparison, the pilchard data were treated according to the Winsor-Walford procedure and the resulting graph is shown in Fig. 23. The slope of the line on the basis of $\bar{n}$, where $\bar{n} = \frac{n_A + n_B}{2}$, is .11. This may be compared with a value of .05 given by Winsor and Walford for their data. Using their formula for the "coefficient of variation" (σ as a % of the mean),

$$\frac{\sigma}{n} = 100\sqrt{\frac{1}{n} + .11}\text{, where } n = \text{number of eggs counted.}$$

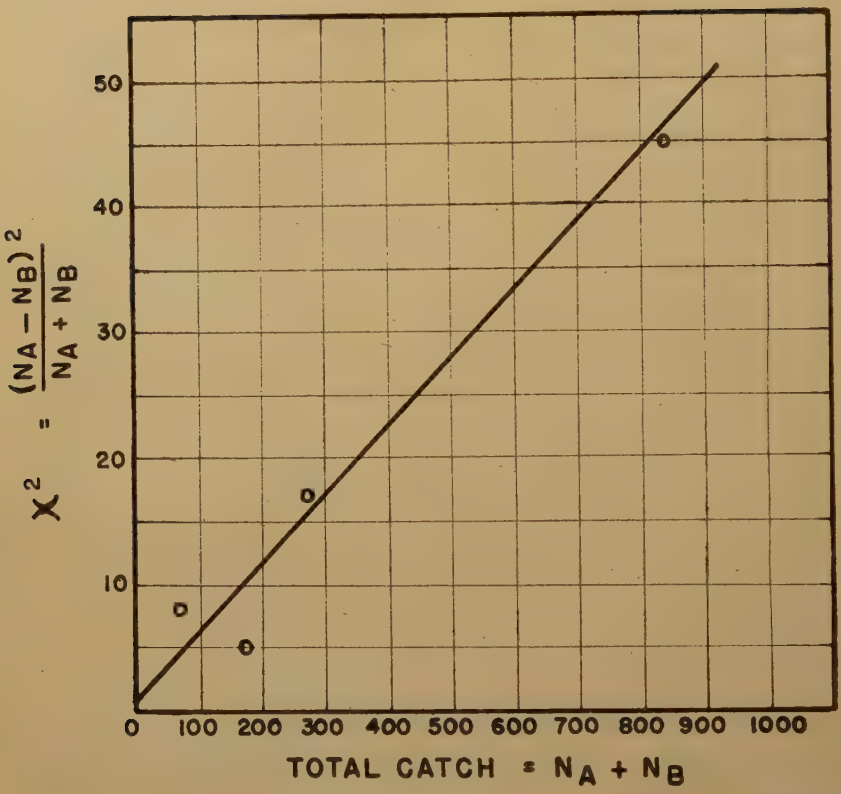

Figure 23. Graph for comparison with Winsor and Walford (1936, fig. 1). The regression line was fitted by inspection, subject to the requirement that the y-intercept be one. Each point represents the average of the values for six stations

Thus for counts of over 100 the value for the pilchard data approaches 33%. This indicates a smaller range of variation than the "half or double" rule given above, and in connection with this comparison of the Winsor-Walford and Winsor-Clarke procedure it is of interest to note that the latter authors state that the estimates of variability given by Winsor and Walford may be too small, since they deal only with discrepancies between members of pairs of hauls.

Returning to a comparison of the pilchard data with the data of Winsor and Walford, the "coefficient of variation" of 33% for the data is somewhat larger than the figure of 22% obtained by them. If this difference is significant, then it must indicate a greater variability between counts from members of pairs of hauls in the pilchard results

than in those of the investigators whose data Winsor and Walford employed. It is probable that this greater variability results largely from the fact that the pilchard egg tows were oblique, while those of the other investigators were vertical. Thus the spatial differences between the members of pairs of pilchard hauls were greater than those between members in the other hauls, and the greater variability of the former may well result from this difference in hauling procedure, rather than in any difference in quality of techniques employed.

DISCUSSION

Although the pilchard data have considerable variability, as shown in the analysis above, the results still appear to be highly significant. This is evidenced by the large "Stations" mean square (Table II), which, as mentioned above, reflects actual spatial and temporal differences between egg concentrations at different stations. Since this mean square is about nine times the *sum* of the items relating to sampling differences (last four items of Table II), it may be inferred that roughly 90 per cent of the variability in egg counts is due to real differences in the concentration of eggs at different stations and only 10 per cent to sampling variability.

One of the objectives of the pilchard egg surveys is the comparison of total egg numbers over certain areas within a season or from season to season, with various numbers of stations involved, depending on the period and area covered. The estimate of σ obtained above (.176) may be used to calculate the fiducial limits of means derived from various numbers of samples. To do so this estimate is divided by the square root of the number of samples to obtain the σ of the mean, and the result is then multiplied by whatever number of σ's it is desired to include within the fiducial limits. This was done for the 2σ limits, and the results were translated to terms of percentage limits for selected numbers of counts (for results, see Table III). As an example of the application of this table, consider the means based on 10 counts (10 1/40 samples from 10 single hauls), with the fiducial limits 78 to 129% (Table III). Thus, if a given group of 10 counts gives a mean count of 500 eggs, any other group of 10 counts having a mean less than 390 eggs (78% of 500) or greater than 645 eggs (129% of 500) could be considered representative of a significantly different egg concentration.

The analysis of variance described above has dealt only with "raw" egg counts, but it is pertinent to mention here that "adjusted" data were also available. Adjustments were based on the calculated volumes of water strained (see Introduction), and were applied in order to remove from the data some of the variability resulting from differ-

TABLE III—Fiducial Limits of Percentage Deviations of Mean Counts, Based on $\pm 2\sigma$ of Logarithmic Values as Calculated from Analysis of Variance. "No. of Counts" Refers to Separate Hauls

No. of Counts	*Lower Limit %*	*Upper Limit %*
1	44	225
2	56	178
3	62	160
4	67	150
5	69	144
10	78	129
15	81	123
20	83	120
30	86	116
40	88	114
50	89	112
75	91	110
100	92	109
150	93	107
200	94	106
250	95	105

ences in these volumes by reducing all egg counts to the basis of a standard volume of water strained. Had the adjustments achieved their purpose, the difference between A and B hauls should be less for adjusted data than for unadjusted data. This was tested by calculating the deviation of the logarithm of the sum of the two counts for each A haul from the corresponding logarithm for the B member of the pair, disregarding the sign of the deviation. The mean deviation for the unadjusted data was .170 and for the adjusted .175. If this minor difference is not due to real differences in horizontal or vertical distribution of the eggs, then this result might be taken to indicate that the current meter data are of questionable value. However, the readings have a utility for purposes other than the reduction of variance of the counts. They permit the calculation of the volume of water strained, and hence the estimation of total egg numbers for certain areas; the readings also make it possible to compare counts from hauls made with different types of gear.

In recapitulation it may be said that a statistical analysis of duplicate laboratory samples from 24 paired plankton hauls for the eggs of the pilchard indicates that most of the variability of egg counts is due to real differences in egg concentration. A study of the purely sampling variability leads to the conclusion that a single count may be considered significantly different from another if it is less than one-half or more than double the other. If groups of counts are used to

calculate means, the significance limits narrow with increasing numbers of counts until, with as many as 250 counts, a difference of five per cent may be considered significant.

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